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Indo-West Pacific and Australian species of Eucalliacidae with descriptions of four new species (Crustacea:Axiidea)

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Abstract Poore, G.C.B. (2021). Indo-West Pacific and Australian species of Eucalliacidae with descriptions of four new species (Crustacea: Axiidea). *Memoirs of Museum Victoria* 80: 1–41.

Surveys of coral reefs and sandy shallow environments in the Indo-West Pacific and Australia have discovered 14 species of Eucalliacidae, of which four are new. All species are diagnosed, and *Andamancalliax arafura* sp. nov., *Eucalliaxiopsis dworschaki* sp. nov., *Eucalliaxiopsis paradoxa* sp. nov. and *Eucalliaxiopsis patio* sp. nov. are described as new. The collection is an opportunity to re-diagnose other species and provide colour photographs of some. *Calliaxina xishaensis* Liu and Liang, 2016, is synonymised with *Calliaxina novaebritanniae* (Borradaile, 1900).

Keywords Crustacea, Axiidea Eucalliacidae, taxonomy, new species

Introduction

Of eight families of callianassid-like Axiidea, Eucalliacidae have the most complicated taxonomic history that was most recently reviewed by Poore et al. (2019). Their revision and the molecular phylogeny on which it was based (Robles et al. 2020) depended in part on extensive collections made in the Indo-West Pacific over the last couple of decades. These collections also made it possible to re-diagnose known species and describe others revealed as new during the molecular study.

Eucalliacidae comprise seven genera, diagnosed by Poore et al. (2019), and 21 species listed by these authors. Six species are from the Atlantic or Mediterranean and two are deep-sea. This contribution deals only with those from coral reefs and shallow environments in the Indo-West Pacific and Australia. Fourteen species are covered here, of which four are described as new.

Methods

Much of the material comes from the Muséum nationale d'Histoire naturelle, Paris (MNHN), including expeditions to Papua New Guinea, Madang Province (PAPUA NIUGINI stations), and New Ireland Province (KAVIENG 2014 stations). Another sizable Indo-West Pacific collection has been accumulated by the Florida Museum of Natural History, University of Florida (UF). Specimens were also examined from Museums Victoria, Melbourne (NMV); the Australian Museum, Sydney (AM); Western Australian Museum, Perth (WAM); and Naturhistorisches Museum, Vienna (NHMW). Unless otherwise stated, station prefixes and numbers belong to systems initiated by the museum holding the material.

Size is expressed as carapace length (cl.), including rostrum, in mm. Individuals marked with an asterisk (*) were sequenced and contributed to molecular analysis (Robles et al., 2020). Diagnoses have been prepared for all species and coded into a DELTA database (Dallwitz, 2010). This database was used to generate the diagnoses presented here; character states in italics diagnose each species in at least one respect from every other species. Colour photographs of fresh specimens were taken in the laboratory shortly after collection by Arthur Anker and Zdeněk Ďuriš. Photographs in figs 12 and 25 were taken using a Leica 205C microscope and the Leica Application Suite multifocus routine.

Eucalliacidae Manning and Felder, 1991

Eucalliinae Manning and Felder, 1991: 781 (misspelling).
Eucalliacinae Sakai, 1999: 108–109.—Sakai, 2018: 734–738 (partim).
Eucalliacidae.—Sakai, 2011: 491.—Sakai and Türkay, 2014: 190 (outdated key to genera).—Sakai, 2018: 734–738.—Poore et al., 2019: 122 (for complete synonymy).

Remarks. The family was diagnosed by Poore et al. (2019). It is recognised most easily by the truncate setose apex of the dactylus of maxilliped 3. Callianopsidae, which also share this feature, differ in that the uropodal exopod lacks a dorsal plate, indicated in eucalliacids by a secondary dense row of stout setae diverging on the upper surface from the anterior margin.

Andamancalliax Sakai, 2011

Andamancalliax Sakai, 2011: 494–495.—Sakai, 2018: 738.—Poore et al., 2019: 126.

Remarks. The genus differs from other eucalliacids in the prominent sharp rostrum and the unequal dissimilar chelipeds, the minor one having elongate fingers. The crista dentata of the type species was not illustrated, but in the new species described here, it comprises few sharp long spines in lieu of a row of similar even teeth seen in other genera. Sakai (2011, 2018) stated that the maxilliped 3 lacks an exopod but in the newly discovered female of what appears to be a different species, a small exopod is present. The genus was diagnosed by Sakai (2011) as having the male pleopod 1 biarticulate, but this was changed by Sakai (2018) to pleopod 1 absent. I believe it is biarticulate, as in other eucalliacids, for the reasons given under remarks on the type species.

Andamancalliax andamanica (Sakai, 2002)

Calliax andamanica Sakai, 2002: 463–467, figs 1, 2.—Sakai, 2005: 201.

Andamancalliax andamanica Sakai, 2011: 495.—Sakai, 2018: 738.

Distribution. Thailand, Andaman Sea. Shelf, 31–61 m.

Remarks. Sakai (2002) referred to the holotype of *Calliax andamanica* as female in the description and male in the figure legends. His figure 2B of the "female Plp 1" from the holotype, described as "uniramous, two-articled, distal article bilobed distally", is most probably from an immature male (cf. fig. 16q of male pleopod 1 of *Eucalliaxiopsis dworschaki* sp. nov.).

Andamancalliax arafura sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:1E5B7D96-E101-45B8-AD22-7156C8B29B30

Figures 2, 3

Material examined. Holotype. Australia, NT, Arafura Sea, 9.2055° S, 133.6483° E, 155–158 m, oozy mud (RV *Southern Surveyor* stn 032BS006), AM P.74526 (female, 3.7 mm, without major cheliped).

Description of holotype. Carapace smooth; gastric–abdominal regions together 4.3 times as long as width of these regions together; branchiostegite fully calcified; cervical groove at 0.62 carapace length, scarcely obvious on branchiostegite.

Rostrum acute, strongly tapering, two-thirds length of eyestalk. Anterolateral carapace lobe absent. Thoracic sternite 7 1.6 times as long as wide, with well-defined median sulcus over posterior half, smooth over medial half, weak lateral ridge anterior to coxal articulation crossing pit at quarter of width.

Pleonite 1 without anterior transverse groove, without sternal plates.

Eyestalk 1.8 times as long as greatest width, swollen laterally, tapering distally around cornea, with defined apical lobe; cornea wider than long. Antennular peduncle 1.8 times as long as width of both eyestalks; article 2 twice as long as wide; article 3 as long as article 2; article 3 with ventrolateral row of few setae, continued onto flagellum. Antennal peduncle 2.2 times as long as width of both eyestalks, overreaching antennule peduncle by most of article 5; scaphocerite ovoid, longer than wide; article 4 c. 5 times as long as wide; article 5 0.7 length of article 4. Maxilliped 3 basis with 4 mesial teeth along lower margin, ischium with strongly expanded proximo-lower lobe, tapering to two-thirds of its greatest proximal width; crista dentata of 3 short basal spines, plus 4 long sharp spines, first 2 recurved, last 2 overlapping merus; merus upper margin 1.5 times as long as greatest width; carpus–dactylus together reaching back to mid-ischium; dactylus as wide as long, with setose truncate apex; exopod third length of upper margin of ischium.

Major cheliped missing. Minor cheliped (right) ischium c. 2.8 times as long as distal width, lower margin with sharp subdistal spine; merus twice as long as broad, lower margin convex, unarmed; carpus 1.1 times as wide as upper length, margins carinate; propodus palm tapering, 0.9 times as wide as upper palm length, upper margin rounded, distomesial margin of palm oblique, distolateral margin of palm oblique, with triangular tooth at base of finger; fixed finger twice length of upper margin of palm, lateral cutting edge with proximal sharp oblique tooth, obtuse distal tooth; dactylus as long as fixed finger, 5 times as long as wide at base, cutting edge with obtuse rounded tooth at about two-thirds.

Pereopod 2 merus 2.2 times as long as maximum width; dactylus c. 5 times as long as upper margin of propodus. Pereopod 3 merus 2.3 times as long as maximum width; carpus 1.7 times as long as wide; propodus with lower margin concave, 1.3 times as long as mid-length; dactylus less than half as long as axial length of propodus. Pereopod 4 merus 3 times as long as maximum width; carpus 3 times as long as wide; propodus setose, with long distal spiniform seta among setose margin, as long as dactylus, with 2 long distal setae overlapping dactylus. Pereopod 5 chelate.

Pleopod 1 uniarticulate, tapering. Pleopod 2 endopod 2.6 times as long as wide; appendix interna at midpoint of endopod, reaching two-thirds remaining length of endopod. Pleopod 3 with appendix interna embedded in endopod.

Uropodal endopod ovoid, anterior margin more convex than posterior margin, widest at midpoint, 1.7 times as long as wide, without facial setae; exopod ovate, greatest dimension 1.6 times anterior margin, anterior margin straight, curving into distal margin, sharper curve between distal and posterior margins, with row of blade-like setae on distal posterior margin; dorsal plate defined by weak longitudinal ridge, extending half of exopod width, distal plate margin with a dozen scattered spiniform setae of various sizes. Telson 1.6 times as wide as long, broadest over anterior half, lateral margin evenly curving to posterior margin; posterior margin convex, with posterolateral clusters of long setae; dorsal surface smooth.

Etymology. For the Arafura Sea (noun in apposition).

Distribution. Australia, Arafura Sea. Shelf, 151–158 m.

Remarks. The truncate setose dactylus of maxilliped 3, presence of a dorsal plate, spike-like rostrum and long fingers on the minor cheliped place the new species in *Andamancalliax*. The sole specimen differs from the illustrations of *A. andamanica* in the presence of a short exopod on maxilliped 3, a distal spine on the lower margin of the ischium of the minor cheliped, a tooth on the fixed finger of the minor cheliped, a

Figure 1. Live colour photographs: a, *Calliaxina bulimba*, Papua New Guinea. MNHN-IU-2013-7097; b, c, *C. kensleyi*, Saudi Arabia, UF 36699; d, e, *C. novaebritanniae*, Papua New Guinea, MNHN-IU-2013-7062; f, *Eucalliaxiopsis dworschaki*, French Polynesia, UF 16286; g, *E. dworschaki*, Papua New Guinea, MNHN-IU-2013-7081; h, *E. inaequimana*, French Polynesia, UF 29162; i, *E. inaequimana*, French Polynesia, UF 29208. Photos a, d, e, g: Z. Ďuriš; b, c, f, h, i, A. Anker. Various scales.

more oval uropodal endopod and a less pronounced dorsal plate on the uropodal exopod. The few sharp spines that constitute the crista dentata are unique within Eucalliacidae; the situation in *A. andamanica* was not reported. The dorsal plate of the uropodal exopod of *A. arafura* is less well developed than in *A. andamanica*, which was said to have the dorsal surface carinate and the anterior half elevated.

Calliaxina Ngoc-Ho, 2003

Calliaxina Ngoc-Ho, 2003: 493–494.—Sakai, 2011: 497 (part).—Poore et al., 2019: 126–127.

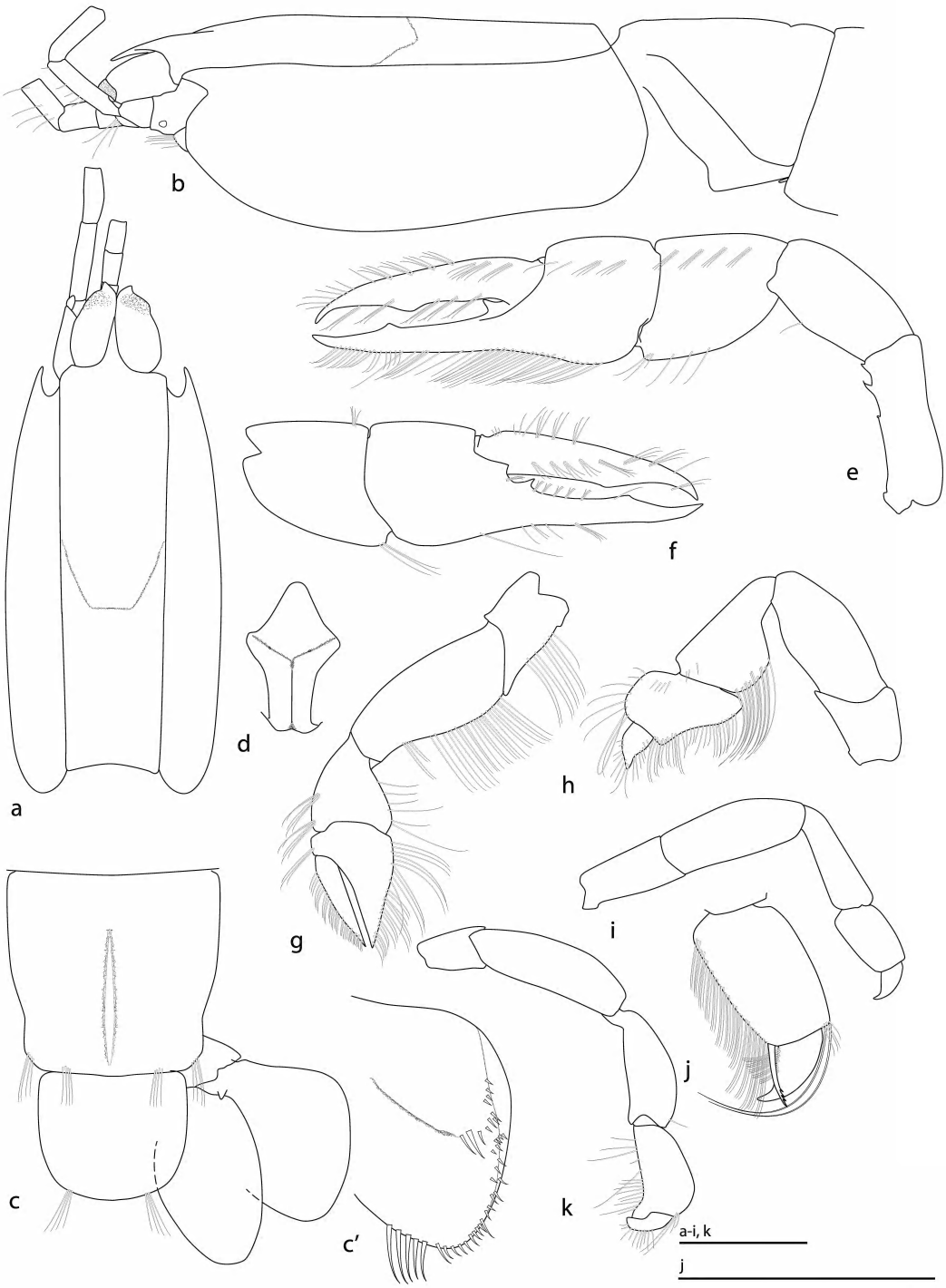

Figure 2. *Andamancalliax arafura* sp. nov. Holotype, Australia, NT, AM P.74526 (female, 3.7 mm): a, b, anterior carapace, eyestalks, antennule, antenna, pleonite 1, dorsal, lateral views; c, pleonite 6, telson, uropod (c', detail of uropod exopod spiniform setae); d, thoracic sternite 7; e, f, minor cheliped (right), mesial, lateral views; g, pereopod 2; h, pereopod 3; i, j, pereopod 4, with detail of propodus, dactylus; k, pereopod 5. Scale bars = 1 mm.

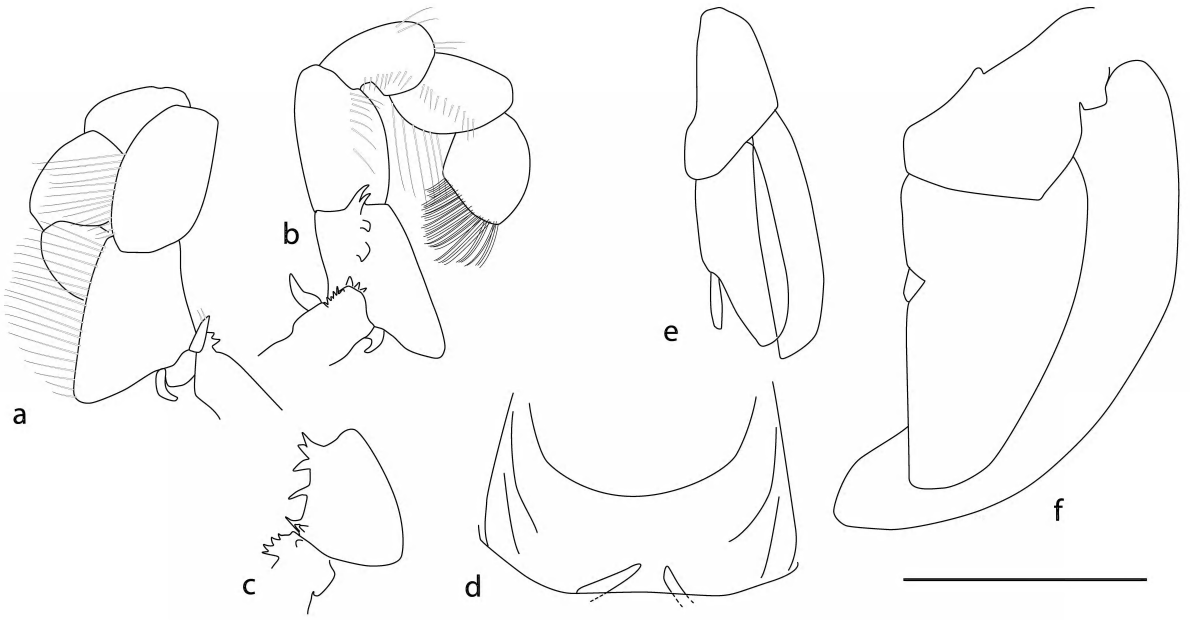

Figure 3. *Andamancalliax arafura* sp. nov. Holotype, Australia, NT, AM P.74526 (female, 3.7 mm): a, b, left maxilliped 3, lateral, mesial views; c, left maxilliped 3, basis, merus, posterior view; d, pleonal sternite 1, pleopod 1; e, f, pleopods 2, 3. Scale bar = 1 mm.

Remarks. *Calliaxina* differs from *Eucalliaxiopsis* in lacking a transverse ridge on the telson, lacking differentiation between male and female major chelipeds, and always possessing an exopod on maxilliped 3, sometimes vestigial (Poore et al., 2019; Robles et al., 2020).

Calliaxina includes the type species, *C. punica* (de Saint Laurent and Manning, 1982) from the western Mediterranean plus four species from the Indo-West Pacific. Separation of the species is difficult because characters defining each have historically been incompletely documented. Juveniles of all species tend to have larger eyes, more acute rostrums and similar telsons, making differentiation on the basis of these characters impossible. Adult males of four species are known; juvenile males of one of these and of the fifth species have presumably immature pleopods 1 (see Poore et al. [2019] and discussions below under *C. bulimba* and *C. novaebritanniae*). Liu and Liang's (2016) key to species included one species here placed in *Eucalliaxiopsis* and relied on the shape of the rostrum and telson, both size-dependent features.

Key to species of *Calliaxina*

1. Maxilliped 3 exopod vestigial 2
– Maxilliped 3 exopod reaching at least third way along ischium 3
2. Major cheliped propodus distomesial margin with setae aligned in 2 groups of c. 10 and c. 6 setae; minor cheliped distomesial margin with setae aligned in 2 scarcely separate groups of c. 20 and c. 8 setae; cheliped merus lower margin with few denticles; Red Sea, Jordan, Saudi Arabia; Madagascar ..... *C. kensleyi* (Dworschak, 2005)
– Major and minor chelipeds propodi distomesial margins with setae aligned in 2 groups of c. 9 setae each; cheliped merus lower margin with 2 or 3 proximal truncated curved teeth and diminishing denticles more distally; Papua New Guinea, SE Australia ..... *C. bulimba* (Poore and Griffin, 1979)
3. Maxilliped 3 exopod overlapping merus (except in juveniles) 4
– Maxilliped 3 exopod reaching half-way along ischium; male pleopod 1 article 2 3 times as long as wide; Japan, East China Sea ..... *C. sakaii* (de Saint Laurent, 1979)
4. Antennule peduncle reaching base of antenna peduncle article 5; male pleopod 1 with broad subapical notch, prominent appendix interna, triangular apex; Mediterranean ..... *C. punica* (de Saint Laurent and Manning, 1982)
– Antennule peduncle reaching midpoint of antenna peduncle article 5; pleopod 1 article 2 with narrow apical notch, short appendix interna, apex prominently curved; Papua New Guinea, Indonesia, NE Australia, Philippines, South China Sea, French Polynesia ..... *C. novaebritanniae* (Borradaile, 1900)

Calliaxina bulimba (Poore and Griffin, 1979)

Figures 1a, 4, 5, 12a, h

Callianassa bulimba Poore and Griffin, 1979: 257, fig. 21.

Calliax bulimba.—de Saint Laurent and Manning, 1982: 222.—Sakai, 1999: 119, fig. 32a–c.—Sakai, 2005: 202.

Calliaxina bulimba.—Sakai, 2011: 499.—Poore et al., 2019: 127, 146, fig. 19g, h.

Eucalliax bulimba.—Dworschak, 2005: fig. 5c, d.

Eucalliax kensleyi.—Sakai, 2017: 1122–1124 (partim), fig. 2D.

Material examined. Australia. Qld, Britomart Reef front, 18° 17' S, 146° 38' E (NMV stn AIMS 57), NMV J12184 (female, 8.7 mm). Rib Reef, 18.48° S, 146.86° E, October 1985, shallow lagoon, 8 m, (M. Riddle stn R/10/1), NMV J71676 (male, 4.6 mm).

Papua New Guinea. Madang Province, lagoon, PAPUA NIUGINI stations: 05° 10.2' S, 145° 50.4' E, 1–3 m (stn PR243), MNHN-IU-2013-7097* (male, 4.5 mm); 05° 10.3' S, 145° 48.5' E, 1–18 m (stn PR213), MNHN-IU-2013-7124 (female, 3.5 mm).

Diagnosis. Sternite 7 with transverse groove visible only laterally, anteromedial lobe rounded. Antennule peduncle reaching to midpoint of antenna peduncle article 5. Maxilliped 3 exopod vestigial, about twice as long as wide. Major cheliped merus, lower margin with 2 or 3 proximal truncate teeth; propodus distomesial margin with setae aligned in 2 similar groups of c. 9 setae each. *Male pleopod 1 article 1 linear, with distal setae; article 2 short, oblique (juvenile form).*

Colour. Exoskeleton translucent white (fig. 1a).

Distribution. Indonesia, Ambon; Papua New Guinea, Madang and New Ireland provinces; Australia, Qld (type locality). Coral reef lagoon, 1–18 m.

Remarks. Poore and Griffin's (1979) simple figures are supplemented here by illustrations of a newly discovered male and female from Australia. The telson is widest proximally, the anterior margins each side of the rostrum are concave, and the distomesial margins of the propodi of the chelipeds bear two widely separate small groups of c. 9 setae each. As is typical of callianassid-like families, the rostrum of small individuals is more acute than in adults and the cornea more swollen. Separation of the anterior and posterior sections of thoracic sternite 7 is weak, with only a slight inclination laterally terminating in a sublateral pit; the posterolateral margin carries groups of c. 6, 7 and 9 long setae (fig. 12h). As figured by Dworschak (2005), pleonite 1 lacks obvious ventral plates but bears two short rows of three or four long setae anterior to the pleopods.

The 4.5-mm male from Papua New Guinea has a pleopod 1 with long distal setae on article 1 and a short simple oblique article 2 (fig. 5d). This is consistent with Poore and Griffin's (1979: fig. 21g) and Dworschak's (2005: fig. 5c, d) illustrations of the much larger holotype (cl. 10 mm) and resembles those of *Eucalliaxiopsis inaequimana* (see Dworschak, 2014: fig. 4j–l), *E. madagassa* (see Ngoc-Ho, 2014: fig. 2S, as *C. thomassini*) and *E. patio* sp. nov. Pleopod 1 of the 4.6-mm male from Australia differs in having a bilobed article 2 with a longitudinal crease and a separate appendix interna (fig. 5b). As argued by Poore et al. (2019), this would appear to be an intermediate form tending towards the more typical eucalliacid male pleopod (e.g., fig. 7h, j). Undeveloped male pleopods 1 are also seen in small juveniles of *C. novaebritanniae* (see below).

The small specimens from Papua New Guinea can be distinguished from the holotype in having an apparently broader uropodal endopod (1.25 times as long as wide vs 1.4 times). They did not possess the fine granular lateral surface in the gape of the cheliped illustrated by Poore and Griffin (1979). Sakai (1999: fig. 32) showed the cobblestone pattern on the lower branchiostegite to be a little more extensive in the holotype from Queensland than on the new material from Papua New Guinea.

This is one of two species with a rudimentary exopod on maxilliped 3, overlooked by Poore and Griffin (1979) but noted on the holotype by Sakai (1999). The exopod bears a few short setae. The other is *C. kensleyi* (Dworschak, 2005); the two were differentiated by Dworschak (2005) but see further comments under *C. kensleyi* below.

Sakai (2017) listed and figured an ovigerous female from Ambon, Indonesia, as *Eucalliax kensleyi* but on biogeographical grounds this is certainly *C. bulimba*.

Calliaxina kensleyi (Dworschak, 2005)

Figures 1b, c, 6, 7, 12b, c, i

Eucalliax kensleyi Dworschak, 2005: 205, figs 1–4, 5a, b.—Sakai, 2017: 1122–1124 (partim), fig. 2A–C, E–G.

Calliaxina kensleyi.—Poore et al., 2019: 125, 127, 146, fig. 19i.

Material examined. Saudi Arabia, Farasan Banks, Marka Island, sandy cay, 18.22055° N, 41.32438° E (stn SAFA-010), UF 36699 (male, 5.9 mm).

Madagascar, Tuléar (now Toliara), Thomassin stn 648, MNHN-IU-2014-10476 (female, 7.8 mm); Thomassin stn 650, MNHN-IU-2016-8086 (female, 6.6 mm). Nosy Bé, MNHN-IU-2016-8084 (male, 7.4 mm).

Diagnosis. Sternite 7 with transverse groove visible only laterally, anteromedial lobe rounded. Antennule peduncle reaching to midpoint of antenna peduncle article 5. *Maxilliped 3 exopod vestigial, about twice as long as wide.* Major cheliped merus, lower margin with 2 or 3 proximal truncate teeth; *propodus distomesial margin with setae aligned in 2 groups of c. 10 and c. 6 setae.* Male pleopod 1 article 2 about 2.5 times as long as wide; appendix interna obsolete.

Colour. Exoskeleton mostly translucent white, gastric region, epistome, upper parts of chelipeds pink (fig. 1b, c).

Distribution. Red Sea (Jordan, Saudi Arabia); western Indian Ocean (Madagascar). Intertidal, shallow sediments.

Remarks. Calliaxina kensleyi shares a vestigial maxilliped 3 exopod with *C. bulimba*. The two species were compared by Dworschak (2005) but the differences he listed are subtle and deserve reinterpretation and addition. The more pronounced rostrum of *C. kensleyi* is subtly so, but juveniles appear to have sharper rostrum in both species. The telson of *C. kensleyi* was

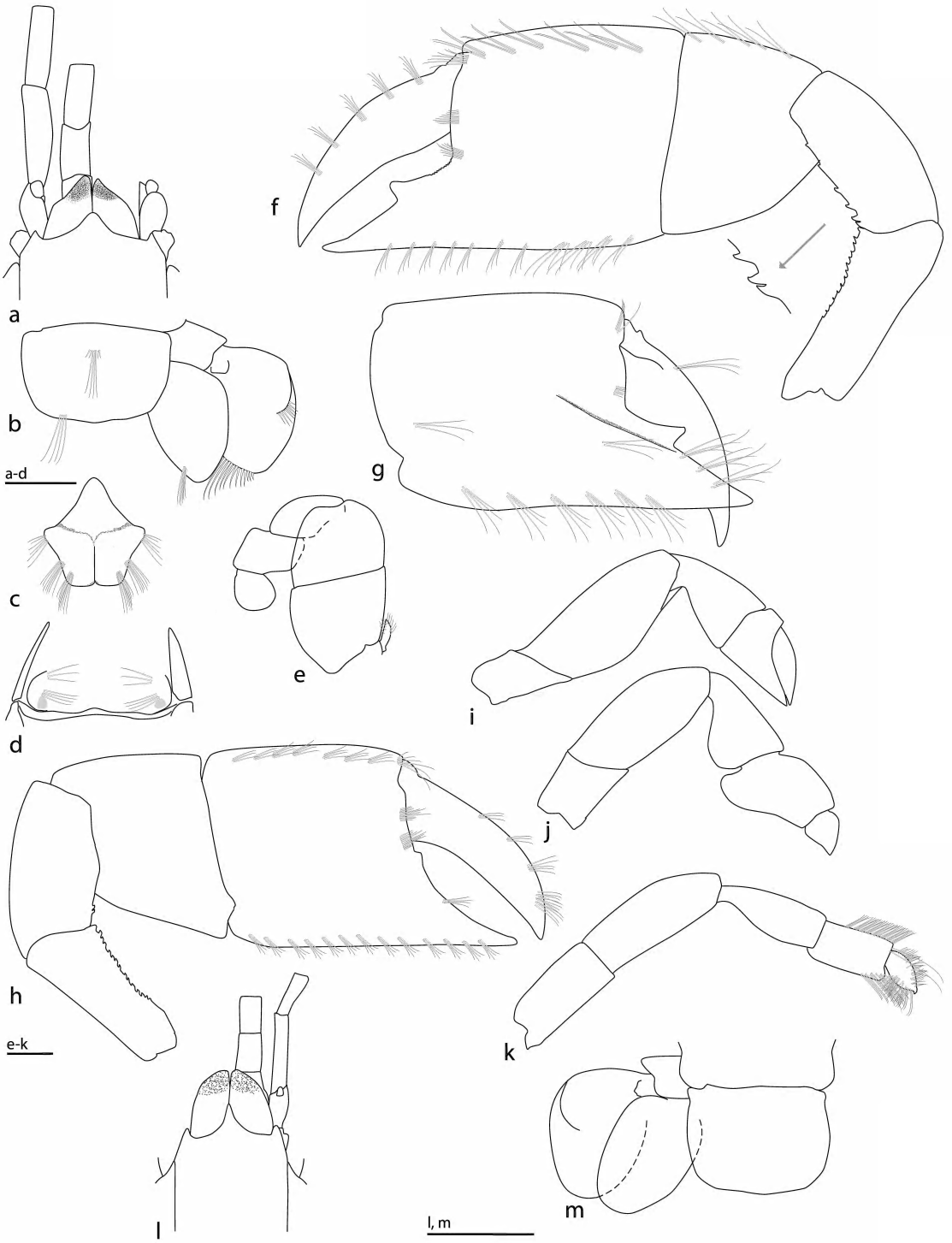

Figure 4. *Calliaxina bulimba*. Australia, Qld, NMV J12184 (female, 8.7 mm): a, anterior carapace, eyestalks, antennule, antenna; b, telson, uropod; c, thoracic sternite 7; d, pleonal sternite 1; e, maxilliped 3; f, g, major cheliped (right), mesial, lateral views; h, minor cheliped (left), mesial view; uropod. Scale bars = 1 mm.

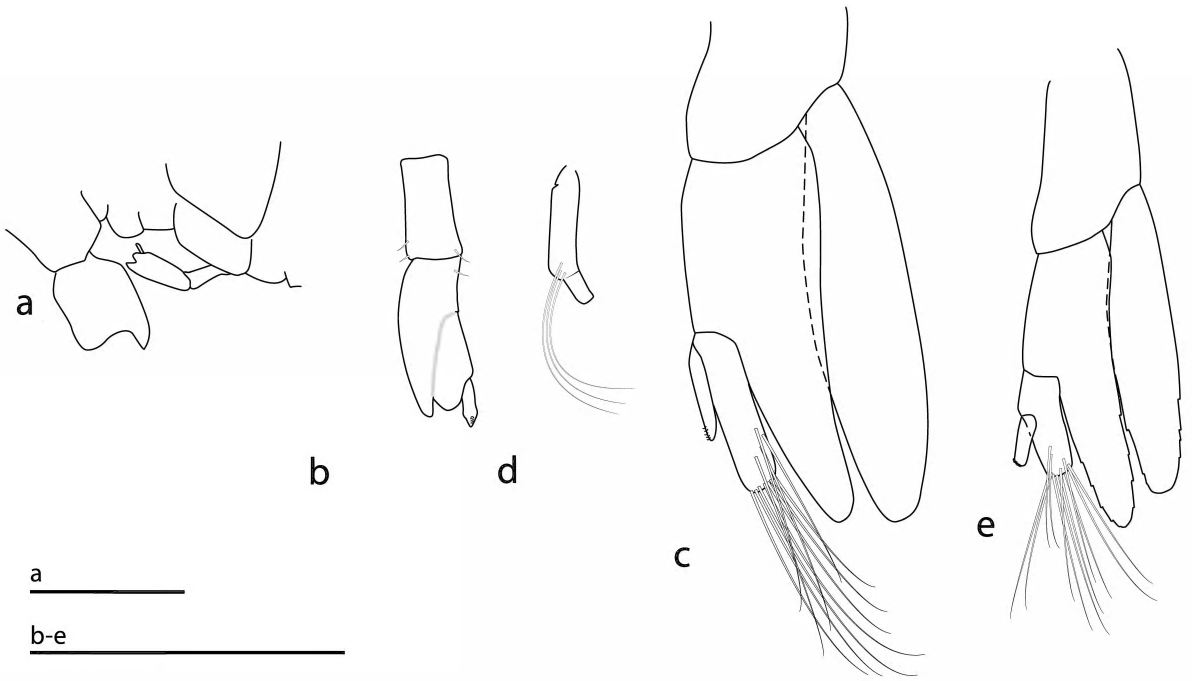

Figure 5. *Calliaxina bulimba*. Australia, Qld, NMV J71676 (male, 4.6 mm): a, left coxa 5, pleonite 1, pleopod 1 in situ, lateral view; b, c, pleopods 1, 2. Papua New Guinea, MNHN-IU-2013-7097 (male, cl. 4.5 mm): d, e, pleopods 1, 2. Scale bars = 1 mm.

said to be widest at its midpoint, whereas that of *C. bulimba* is widest anteriorly; this difference is less obvious in smaller specimens. The uropodal exopod is oval in *C. kensleyi*, more tapering in *C. bulimba*, but again less clear in smaller specimens. In both species, the major cheliped (the slightly wider one) has a tooth on the fixed finger, whereas the minor cheliped does not, with the apparent exception of the paratype of *C. kensleyi*.

Despite their obvious morphological similarity, *Calliaxina kensleyi* and *C. bulimba* were not the two most phylogenetically related of the four species in Robles et al.'s (2020) study. *Calliaxina kensleyi* was sister species to *C. novaebritanniae*, and these two more related to *C. sakaii*, which if true suggests that the vestigial maxilliped 3 exopod has evolved twice. Ovoid plates are visible on the sternite of pleonite 1 (fig. 6c) but absent in *E. bulimba* (fig. 4d).

Dworschak (2005) did not describe the dentition of the lower margin of the merus of the chelipeds of *C. kensleyi*; in the new material there are few proximal denticles (fig. 6e, f). All specimens of *C. bulimba* possess two or three proximal truncated curved teeth and diminishing denticles more distally (fig. 4f). The distomesial face of the propodus of the chelipeds has two rows of submarginal setae in both species. On the major cheliped of *C. kensleyi*, these setae align in two separate groups of c. 10 and c. 6 setae (figs 6d, 12c); on the minor cheliped, the setae align in two scarcely separate groups of c. 20 and c. 8 setae (fig. 6f; Dworschak, 2005: fig. 3a, c). On both chelipeds of *C. bulimba*, distomesial setae align in two widely separate groups of c. 9 setae each (fig. 4h). The distolateral propodus of the chelipeds is granulated in a concavity at the base of the fingers in some individuals of both species but is absent on others, especially smaller specimens.

The two males identified here as *C. kensleyi* possess a male pleopod 1 typical of several species of *Calliaxina* and *Eucalliaxiopsis*: *C. novaebritanniae*, *C. paradoxa*, *C. punica*, *C. sakaii*, *Eucalliaxiopsis jonesi* (Heard, 1989), *E. mcilhennyi* (Felder and Manning, 1994) and *E. panglaoensis* (all with a broad article 2, appendix interna and curved apex; see fig. 7h, j and earlier papers (Dworschak, 2006, 2014; Felder and Manning, 1994; Heard, 1989; de Saint Laurent and Manning, 1982;). As noted above, the male pleopod 1 of *C. bulimba* differs from all of these, its second article lacking an appendix interna and distal curved apex. The appendix masculina on pleopod 2 of *C. kensleyi* is narrower than that of *C. bulimba*.

Sakai (2017) included *C. kensleyi* in *Eucalliax* although

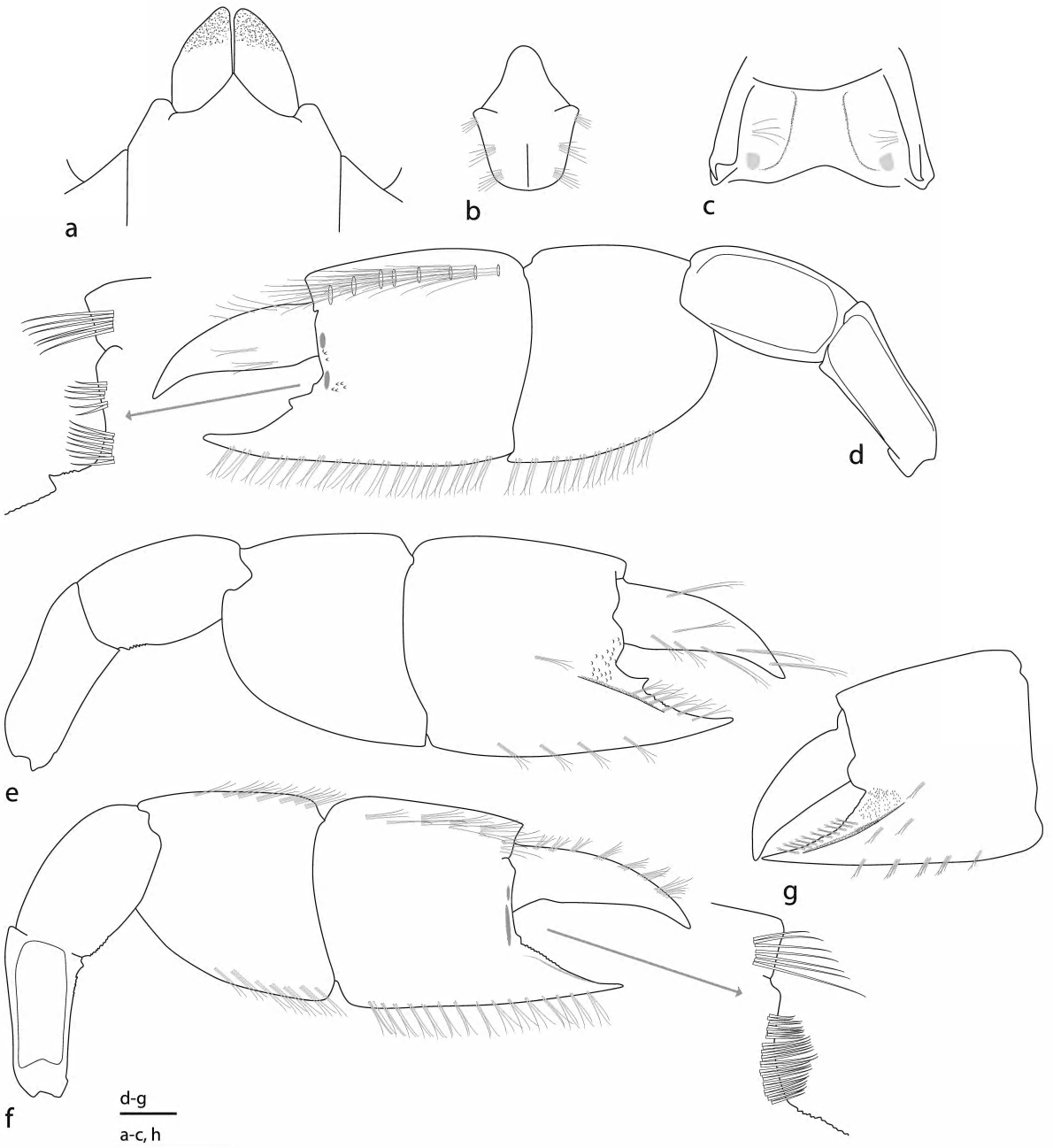

Figure 6. *Calliaxina kensleyi*. Madagascar, MNHN-IU-2014-10476 (female): a, anterior carapace, eyestalks; b, thoracic sternite 7; c, pleonal sternite 1 (anterior uppermost); d, e, major cheliped (right), mesial, lateral views, with detail of mesial setae on propodus; f, g, minor cheliped (left), mesial, lateral views, with detail of mesial setae on propodus. Scale bars = 1 mm.

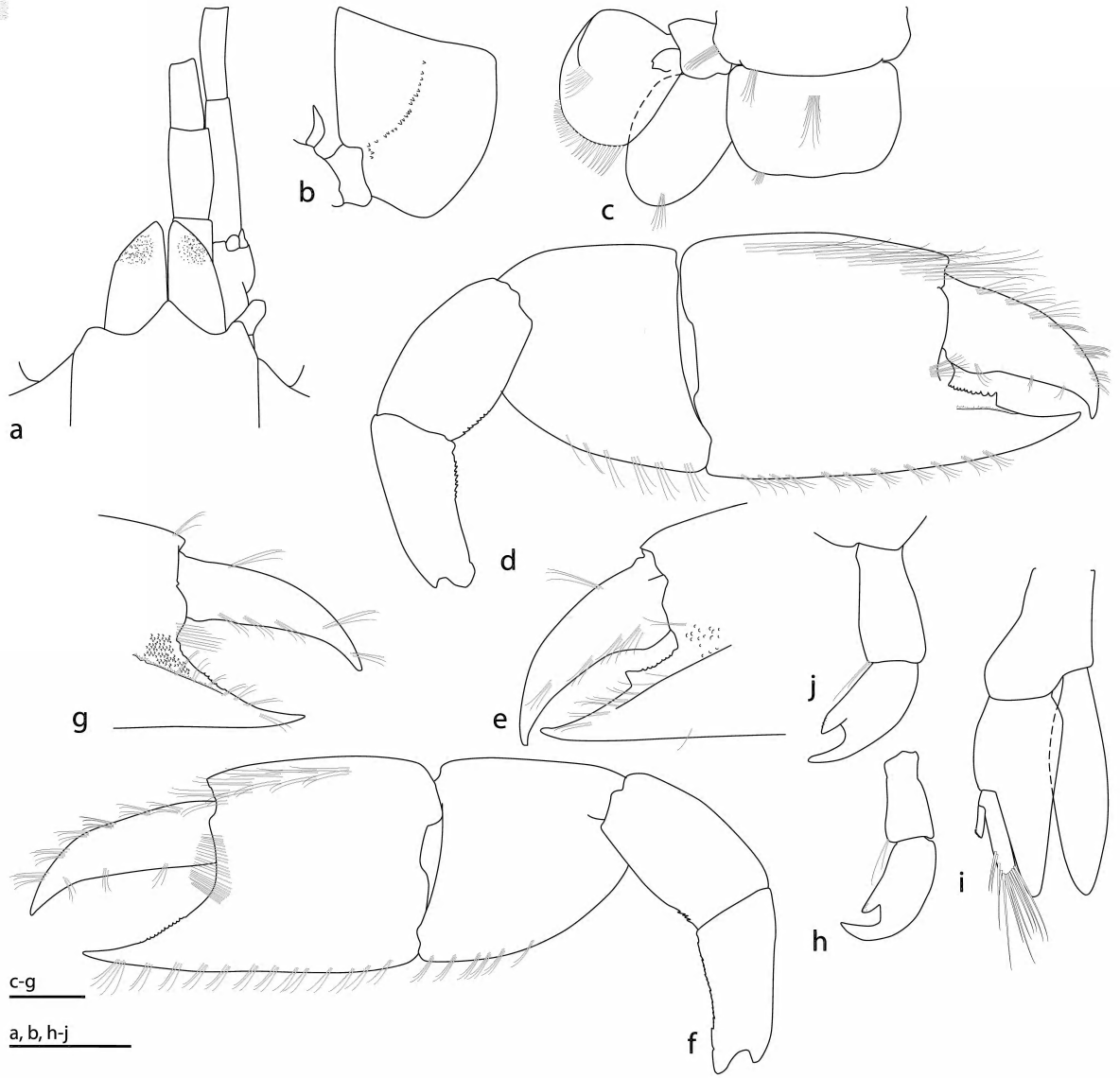

Figure 7. *Calliaxina kensleyi*. Saudi Arabia, UF 36699 (male): a, anterior carapace, eyestalks, antennule, antenna; b, maxilliped 3, exopod, basis, ischium; c, telson, uropod; d, major cheliped (left), mesial view; e, major cheliped fingers (left), lateral view; f, minor cheliped (right), mesial view; g, minor cheliped fingers (right), lateral view; h, i, pleopods 1, 2. Madagascar, MNHN-IU-2014-8084 (male): j, pleopod 1. Scale bars = 1 mm.

the species has all the features of *Calliaxina*, however diagnosed. His figure 2A–C, E–G of material from the Red Sea resembles the types from the nearby type locality, Aqaba. His figure 2D of the cheliped of a female from Ambon has a curiously triangular carpus. The location suggests *C. bulimba*, a species he did not mention. He referred to *E. kensleyi* as being from Aqaba and Moreton Bay (*Calliaxina bulimba* is from Moreton Bay, Qld) but listed the type locality as Alona Beach, the Philippines (the type locality of *E. panglaoensis* Dworschak, 2006). The species was not listed by Sakai (2011).

Calliaxina novaebritanniae (Borradaile, 1900)

Figures 1d, e, 8–10, 12d, e, j

Callianassa novae-britanniae Borradaile, 1900: 419, pl. 39 figs 14a–d.

Callianassa (*Callichirus*) *novae-britanniae*.—Borradaile, 1903:

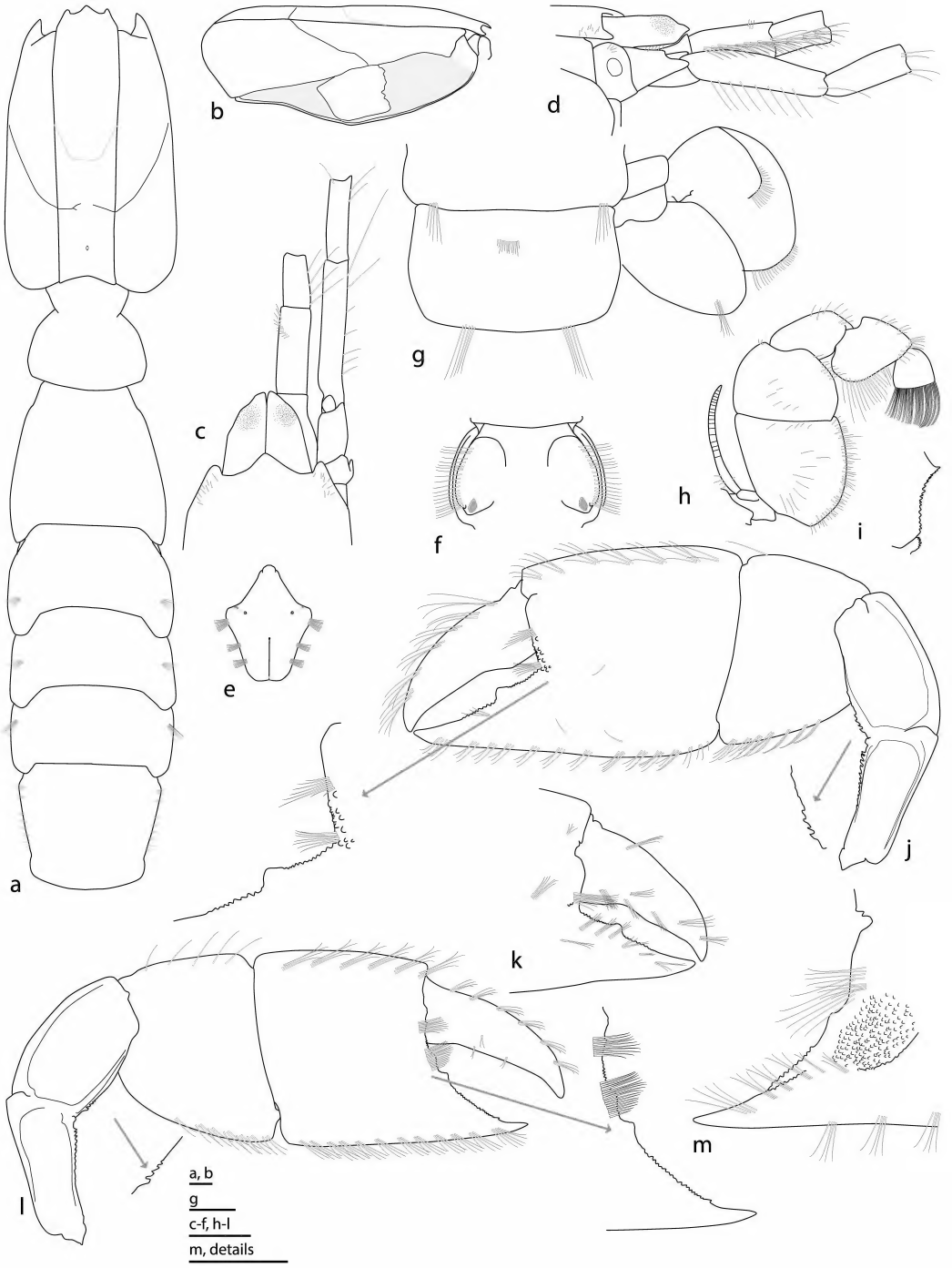

Figure 8. *Calliaxina novaebritanniae*. Australia, NMV J71677 (female, 11.5 mm): a, carapace, pleon, dorsal; b, carapace, lateral; c, d, anterior carapace, eyestalks, antennule, antenna, dorsal and lateral views; e, thoracic sternite 7; f, pleonal sternite 1; g, telson, uropod; h, maxilliped 3; i, maxilliped 3, crista dentata, basis, ischium; j, major cheliped (right), mesial with detail of merus margin, distal propodus; k, major cheliped (right), distal propodus, dactylus, lateral; l, minor cheliped (left), mesial view, with detail of merus margin, distal propodus; m, minor cheliped (left), fixed finger, lateral. Scale bars = 1 mm.

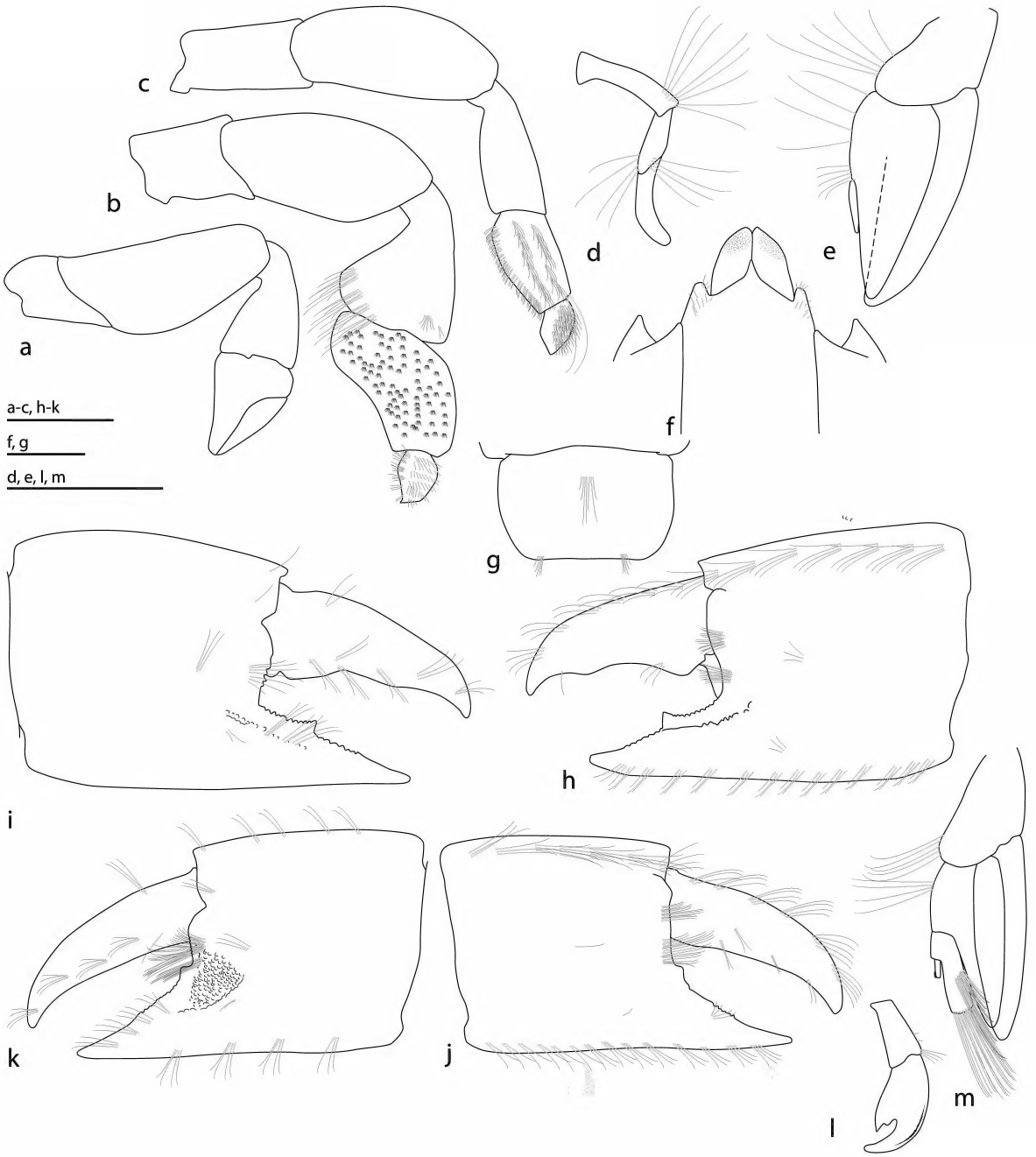

Figure 9. *Calliaxina novaebritanniae*. Australia, NMV J71677 (female, 11.5 mm): a–c, pereopods 2–4; d, e, pleopods 1, 2. NMV J71678 (male, 8.7 mm): f, anterior carapace, eyestalks; g, telson; h, i, major cheliped (right), propodus, dactylus, mesial and lateral; j, k, minor cheliped (left), propodus, dactylus, mesial and lateral; l, m, pleopods 1, 2. Scale bars = 1 mm.

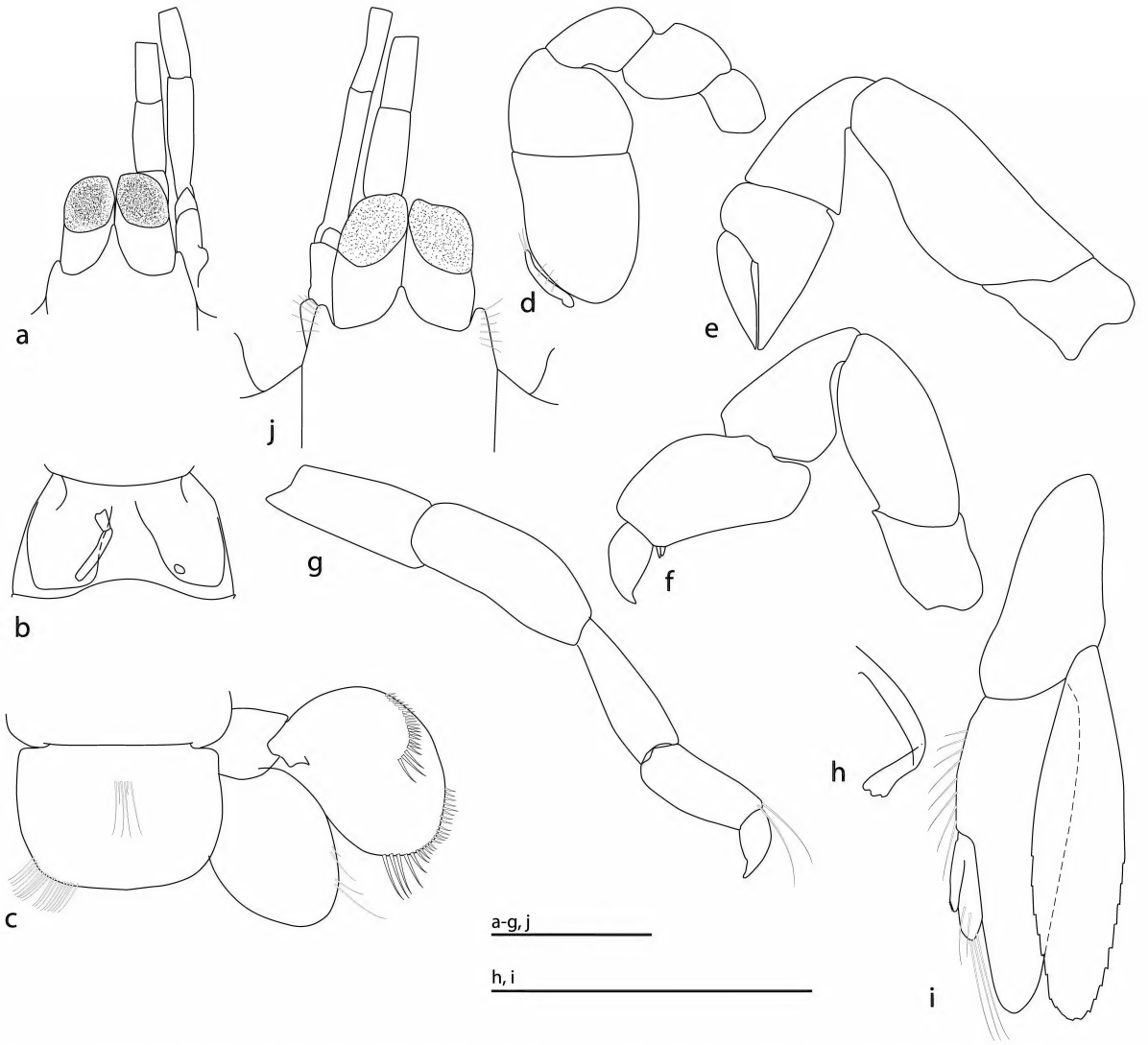

Figure 10. *Calliaxina novaebritanniae*. Papua New Guinea, MNHN-IU-2014-8837 (male, 4.0 mm): a, anterior carapace, eyestalks, antennule, antenna; b, pleonal sternite 1, right pleopod 1(anterior uppermost); c, telson, uropod; d, maxilliped 3; e–g, pereopods 2–4; h, i, pleopods 1, 2. French Polynesia, UF 23954 (female, 5.1 mm): j, anterior carapace, eyestalks, antennule, antenna. Scale bars = 1 mm.

547.— Borradaile, 1904: 753.—De Man, 1928a: 48.—De Man, 1928b: 29, 92, 93, 114 (part).

Calliax novaebritanniae.—de Saint Laurent and Manning, 1982: 211–224, figs 1c, 2b, 6c.—Sakai, 2005: 202.

Paraglypturus novaebritanniae.—Sakai, 1999: 123, fig. 32d–f.

Calliaxina novaebritanniae.—Ngoc-Ho, 2003: 493.—Sakai, 2011: 500–501.—Dworschak, 2018: 17–19, fig. 1b, c (synonymy, notes).—Poore et al., 2019: 126, 127, 146.—Robles et al., 2020.

Calliaxina xishaensis Liu and Liang, 2016: 83–87, figs 1, 2. **Syn. nov**.

not *Callianassa (Callichirus) novaebritanniae*.—Sakai, 1966: 161–171 (record from Japan = *C. sakaii* [de Saint Laurent, 1979]).

not *Callianassa (Callichirus) novaebritanniae* var.—De Man, 1928b: fig. 20 (= *C. punica* [de Saint Laurent and Manning, 1982] fide de Saint Laurent and Manning [1982]).

Material examined. Papua New Guinea. Madang Province, lagoon, 05° 10.2' S, 145° 50.4' E, 1–3 m (PAPUA NIUGINI stn PR243), MNHN-IU-2013-7062* (ovigerous female, cl. 8.8 mm). New Ireland Province, Nago Island, 02° 36.3' S, 150° 46.2' E, 3–12 m (KAVIENG 2014 stn KR06), MNHN-IU-2014-8837* (male, 4.0 mm); MNHN-IU-2013-7941* (female, c. 4.0 mm).

French Polynesia, Moorea Island, NW motus, in channel between

islands and beach, 17.488393° S, 149.91342° W (stn BIZ-148), UF 23954 (female, 5.1 mm)

Australia, Qld, Great Barrier Reef. Myrmidon Reef, 18.27° S, 147.38° E, October 1985: lagoon with "*Callianassa*" mounds, 8 m, (M. Riddle stn M/10/1), NMV J71677 (female, 11.6 mm); NMV J71678 (male, 8.7 mm); NMV J71669 (2 males, 8.4 mm; 6 ovigerous females, 6.9–10.3 mm; 1 female, 9.4 mm). Myrmidon Reef, 18.27° S, 147.38° E, October 1985: shallow lagoon, 4 m, (M. Riddle stn M/10/2), NMV J71670 (2 males, 11.1 mm; 3 ovigerous females, 10.4 mm); outer reef flat, 2 m, (M. Riddle stn M/10/3), NMV J71673 (3 males). Rib Reef, 18.48° S, 146.86° E, October 1985: reef flat, 4 m, (M. Riddle stn R/10/2), NMV J71671 (4 males; 16 females). reef flat, 8 m, (M. Riddle stn R/10/1), NMV J71675 (6 males, smallest 5.5 mm; 4 females). Lizard Island, 50 m W of Loomis beach, 14.6816° S, 145.4515° E, (stn AUST-ST-036), UF 16947 (ovigerous female, 9.0 mm). Lord Howe Island, Old Settlement Beach, 31.5° S, 159.1° E (stn LHI 2017 059), AM P.100430 (2 males, 11.9 mm, 14.6 mm).

Diagnosis. Sternite 7 with transverse groove visible only laterally, anteromedial lobe rounded. Antennule peduncle reaching to midpoint of antenna peduncle article 5. *Maxilliped 3 exopod reaching third to half-way along ischium (juveniles only) or reaching to mid-merus*. Major cheliped merus, lower margin with 2 or 3 proximal truncate teeth; propodus distomesial margin with setae aligned in 2 similar groups of c. 9 setae each. *Male pleopod 1 article 2 twice as long as wide*; appendix interna prominent.

Description of female. Carapace scattered with small shallow depressions; gastric–abdominal regions together 4.6 times as long as wide; branchiostegite calcified over dorsal half, separate from wide ventral uncalcified anterior region and narrower triangular uncalcified posterior section, the two separated from each other by squarish calcified plate; posteroventral area without small calcified plates; cervical groove at 0.57 carapace length, scarcely obvious on branchiostegite; cardiac sulcus at 0.73 carapace length, not meeting mid-dorsally, extending obliquely anteroventrally to lower limit of calcified branchiostegite.

Thoracic sternite 7 1.35 times as long as wide, with well-defined median sulcus over posterior third, smooth over medial half, lateral ridge anterior to coxal articulation ending in pit at quarter of width, with 3 posterolateral clusters of long setae.

Rostrum broadly triangular, length about 0.25 width of eyestalks. Anterolateral carapace lobe half as long as rostrum, with rounded apex, dorsal anterolateral margin oblique in dorsal view as far back as anterodorsal angle of branchiostegite, with c. 10 submarginal dorsal setae. Pleonites 1–6 lengths relative to cl: 0.42 : 0.47 : 0.30 : 0.30 : 0.32 : 0.47; pleonite 1 with strong dorsal transverse groove, with pair of oval sternal plates supporting pleopods, each with lateral row of c. 20 setae; pleonites 3–5 with lateral tufts of setae; pleonite 6 with 8 lateral rows of setae.

Eyestalk 1.85 times as long as wide at base, tapering slightly to cornea, then more rapidly to subacute apices, sometimes with minute mesiodorsal tubercle; cornea round, slightly domed, 0.6 width of maximum eyestalk width. Antennular peduncle 2.5 times as long as width of both eyestalks; article 2 3 times as long as wide; article 3 0.6 length of article 2; articles 2 and 3 with ventrolateral row of long setae, continued onto flagellum. Antennal peduncle 3.2 times as long as width of both eyestalks, overreaching antennule peduncle by all of article 5; scaphocerite ovoid, longer than wide; article 4 c. 7 times as long as wide; article 5 half as long as article 4. Maxilliped 3 exopod reaching to midpoint of merus; ischium with convex mesial margin, expanding from narrow proximomesial corner; ischium–merus 1.8 times as long as greatest width; crista dentata of c. 25 even denticles on basis and ischium; carpus–dactylus together as long as ischium–merus.

Chelipeds subequal, major 1.1 length of minor. Major cheliped ischium c. 2.2 times as long as distal width, lower margin with truncate denticles becoming more distinct distally; merus 2.6 times as long as broad, lower margin with 4–5 truncate proximal denticles, diminishing distally; carpus 1.5 times as wide as upper length, margins carinate; propodus greatest width in middle of palm, as wide as upper palm length, distomesial margin of palm with 2 submarginal groups each of c. 8 setae plus nearby granules, distolateral margin of palm with submarginal group of c. 10 setae between fingers; fixed finger half as long as upper margin of palm, cutting edge with microdenticles over proximal half, blunt triangular tooth third way along; dactylus as long as fixed finger, twice as long as wide at base, cutting edge concave over proximal half; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers.

Minor cheliped ischium c. 2.3 times as long as distal width, lower margin with truncate denticles becoming more distinct distally; merus 1.7 times as long as broad, lower margin with 4–5 truncate proximal denticles, diminishing distally; carpus 1.5 times as wide as upper length, margins carinate; propodus palm more evenly wide than major, 1.1 times as wide as upper palm length, distomesial margin of palm with 2 submarginal groups of c. 10 and c. 12 setae, distolateral margin of palm with submarginal group of c. 10 setae, plus 2 smaller groups further from margin between fingers; fixed finger 0.4 times as long as upper margin of palm, mesial cutting edge with microdenticles, blunt proximal tooth, lateral cutting edge microdenticulate defining edge of lateral concavity at base of fixed finger, filled with granules; dactylus overreaching fixed finger, 3 times as long as wide at base, cutting edge curved; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers.

Pereopod 2 merus 2.2 times as long as maximum width; dactylus c. 3 times as long as upper margin of propodus. Pereopod 3 merus twice as long as maximum width; carpus as long as wide; propodus with strongly concave lower margin, twice as long as mid-length; dactylus 2.5 times axial length of propodus. Pereopod 4 merus 2.3 times as long as maximum width; carpus 2.5 times as long as wide; propodus typically setose, with 2 long distal setae overlapping dactylus.

Pleopod 1 article 1 without distal projection beyond article 2; article 2 longer than article 1. Pleopod 2 endopod 2.5 times as long as wide; appendix interna about quarter length of endopod.

Uropodal endopod ovoid, anterior margin more convex than posterior margin, widest about third way along, 1.5 times as long as wide, with subdistal facial group of c. 8 long setae; exopod 2.4 times as wide as long (length measured from peduncle to anterior point of dorsal plate), distal and posterior margins typically setose, with c. 20 blade-like setae near end of posterior margin; dorsal plate extending almost over half of

exopod width, posterior margin with spiniform setae. Telson 1.7 times as wide as long, broadest at mid-length, posterolateral corner more sharply rounded than lateral and posterior margins; posterior margin convex, with lateral lines of long setae; dorsal surface with median row of long setae at anterior quarter.

Adult male. As in female except as follows. Major cheliped propodus, distomesial margin of palm with 2 submarginal groups each of c. 8 setae, fixed finger with proximal mesial and lateral granulate ridges; dactylus cutting edge with basal blunt tooth.

Minor cheliped propodus, distomesial margin of palm with 2 submarginal groups of c. 12 and c. 15 setae, distolateral margin of palm with submarginal groups of c. 30 and c. 15 setae; lateral concavity at base of fixed finger, filled with numerous granules.

Pleopod 1 article 1 twice as long as greatest width; article 2 2.3 times as long as wide, appendix interna acute, without hooks, subdistal lobe small, distal curved lobe acute, occupying about third of whole. Pleopod 2 endopod 2.3 times as long as wide; appendix masculina attached at c. 0.4 of length, 3.5 times as long as distal width, distal margin convex-truncate reaching 0.9 length of endopod, with c. 20 facial setae near midpoint, c. 15 subdistal setae; appendix interna rod-like, with hooks, about fifth length of appendix interna.

Variation. Branchiostegite always divided by oblique longitudinal edge between calcified dorsal region and variously uncalcified ventral region, always with midventral rectangular plate, sometimes with posteroventral tessellated pattern (Sakai, 1999: fig. 32e), sometimes more or less calcified, often not calcified. Rostrum more acute in smaller specimens (figs 3a, j). Cornea larger in smaller specimens (fig. 3j). Maxilliped 3 exopod reaching mid-ischium in some small specimens. Minor cheliped propodus fixed finger proximal concavity variously granulate.

Colour. Exoskeleton mostly translucent white, middle of branchiostegites pink (fig. 1d, e).

Distribution. Papua New Guinea, Madang, New Britain (type locality) and New Ireland provinces; Indonesia, Sulawesi, Bali; Australia, N Qld; Philippines, Pulawan; French Polynesia. Lagoon sediments, to 12 m.

Remarks. Calliaxina novaebritanniae is unique in the Indo-West Pacific in having the exopod of maxilliped 3 reaching to the middle of the merus in adults. Small genetic differences were found between the pair from Nago Island (New Britain), one from Madang, one from Palawan, Philippines (NHMW 25366), and one from Indonesia (NHMW 25783) (Robles et al., 2020). Nago Island and Madang, Papua New Guinea, are not far distant, west and east respectively, from the type locality. Morphological differences between them, the female from French Polynesia and the large collection from the Great Barrier Reef, Australia, are small. The telson and uropod of adults are the same, all have a sulcus on the carapace. The maxillipedal 3 exopod reaches to mid-merus except in two small specimens where it is shorter than in adults, a phenomenon noted by Liu and Liang (2016) in *C. xishaensis.* The rostrum is sharper and the eyestalks more rounded in smaller specimens. Article 2 of pleopod 1 of the holotype has two similar distal lobes on its inner margin (one the appendix interna) and an apex strongly curving mesially (de Saint Laurent and Manning, 1982: fig. 6). The appendix interna and second subdistal lobe are less developed in all the Australian males in this collection (fig. 9l). A juvenile male from Papua New Guinea has a simple pleopod 1 with three obsolete distal lobes (fig. 10h), indicating that this limb metamorphoses with maturity. The male pleopod 2 has a broad appendix masculina, with distal and subdistal clusters of long setae, and appendix interna midway on the endopod (fig. 10i).

Calliaxina novaebritanniae co-occurs in one sample from the Great Barrier Reef with individuals of *C. bulimba* from which it is difficult to distinguish at first glance. However, the exopod of maxilliped 3 reaches to the middle of the merus in most *C. novaebritanniae* but is vestigial in all *C. bulimba.* The eyestalks of *C. novaebritanniae* are narrower than in *C. bulimba* (almost twice as long as wide vs 0.8 times as long as wide in adults), the antennal peduncles are narrower (antennular peduncle article 2 3.5 times as long as wide vs twice; antennal lpeduncle article 4 6 times as long as wide vs 3 times). The telson of *C. novaebritanniae* is widest at its midpoint whereas in *C. bulimba* it tapers from the base, although the taper is less obvious in juveniles. Pereopods of *C. novaebritanniae* are relatively broader than in *C. bulimba* (meri of pereopods 2 and 3, 2.5 and 2.0 times as long as wide vs 2.2 and 2.4 times). The rostrum is more acute in larger *C. novaebritanniae* than in similarly sized *C. bulimba* but is more acute in small specimens of both species.

Borradaile (1900) based his description on a single male of total length 37 mm from New Britain (Papua New Guinea). The holotype was illustrated by Borradaile (1900), de Saint Laurent and Manning (1982) and Sakai (1999). Notwithstanding the species' long and complicated synonymy, the material listed here and that from the Philippines and Indonesia (Dworschak, 2018) are the first reported since. De Man (1928a) described and illustrated a specimen he identified as a variety of *C. novaebritanniae*; this was described as *Calliax* (now *Calliaxina*) *punica* by de Saint Laurent and Manning (1982), type locality, Salammbo, Gulf of Tunis. De Man (1928b) identified material from the Maldives as *C. novaebritanniae*; this was identified by Sakai (1999) as *Calliax* (now *Eucalliaxiopsis*) *aequimana* (Baker, 1907) but is almost certainly *E. inaequimana* (Dworschak, 2014).

In as far as can be decided from descriptions, *C. novaebritanniae* is indistinguishable from *C. xishaensis* Liu and Liang, 2016. The latter was described from two females from the South China Sea, not far from Palawan, Philippines. A specimen from this locality (NHMW 25366) was found to be genetically similar to those from Papua New Guinea (the type locality) and Indonesia, suggesting that the species has a wide distribution. *Calliaxina xishaensis* is here synonymised with *C. novaebritanniae*. *Calliaxina sakaii* is close by in Japan but is morphologically and genetically quite remote (see below and Robles et al., 2020).

Sakai's (1999) designation of the holotype as a lectotype was unnecessary.

Calliaxina sakaii de Saint Laurent *in* de Saint Laurent and Le Loeuff, 1979

Figures 11, 12f, g

Callianassa (*Callichirus*) *novaebritanniae*.—Sakai, 1966): 161–168, figs 1–4.

Calliax sakaii de Saint Laurent *in* de Saint Laurent and Le Loeuff, 1979: 95.—de Saint Laurent and Manning, 1982: 212, 222–223, figs 1g, 2c.—Sakai, 1987: 305–306.—Sakai, 2005: 203.

Paraglypturus sakaii.— Sakai, 1999: 124, fig. 33d, e.

Calliaxina sakaii.—Ngoc-Ho, 2003: 489, 493, 496, fig. 20J.—Sakai, 2011: 502.—Sakai, 2018: 739.

Material examined. Japan, Tomioka, MNHN Th312 (holotype male, 10 mm), MNHN Th313 (female), NMV J59763 (male, 6.7 mm; female, 7.0 mm; ex ULLZ-8894*).

Diagnosis. Sternite 7 with complete transverse V-shaped groove, anteromedial lobe acute. Antennule peduncle reaching to base of antenna peduncle article 5. Maxilliped 3 exopod reaching third to half-way along ischium. Major cheliped merus, lower margin with several proximal teeth; propodus distomesial margin with setae aligned in 4 groups of 10, 5, 7 and 4 setae. Male pleopod 1 article 2 3 times as long as wide; appendix interna prominent.

Remarks. Differences between *C. sakaii* and the more widespread *C. novaebritanniae* were confirmed by re-examination of the holotype and more recently collected material. The male pleopod 1 has a bilobed proximal lobe and pleonal sternite 1 has a pair of oval plates supporting the pleopods, both similar to *C novaebritanniae*. *Calliaxina sakaii* differs from *C. novaebritanniae* in the exopod of maxilliped 3 reaching half the length of the ischium (vs overlapping the merus), a more acute rostrum, fully calcified branchiostegites (vs weakly chitinised over the lower half), having a deep sharp transverse groove on thoracic sternite 7 (vs an obsolete ridge) and the posterior margin of the telson concave (convex). The distomesial margin of the propodus of the major cheliped has four groups of 4–10 submarginal setae, two groups on the minor cheliped (vs two groups on both chelipeds). A lateral concavity at the base of the fixed finger is defined by a lower ridge on both chelipeds.

The species was described briefly in footnote number 14 by M. de Saint Laurent alone in de Saint Laurent and Le Loeuff (1979).

Eucalliaxiopsis Sakai, 2011

Eucalliaxiopsis Sakai, 2011: 503–504.—Poore et al., 2019: 127–128 (synonymy).

Remarks. Eucalliaxiopsis differs from *Calliaxina* in having a strong ridge across the telson, lacking an exopod on maxilliped 3 (with one exception), the appendix masculina overlapping the endopod of pleopod 2, and in the major cheliped of the male usually being more robust, the palm longer and wider, than that of the female. In *Calliaxina*, the telsonic ridge is absent or obsolete, maxilliped 3 always possesses an exopod, the appendix masculina does not reach the apex of the endopod of pleopod 2, and chelipeds of males and females are not differentiated from each other nor scarcely from the minor chelipeds. In as much as can be deduced from published illustrations, the lower margin of the merus of the chelipeds is smooth or with small tubercles at its midpoint in *Eucalliaxiopsis*, whereas this margin bears small proximal truncate teeth in *Calliaxina*. The post-rostral dorsal area of some species of *Eucalliaxiopsis* (*E. aequimana, E. madagassa*) has a broad median longitudinal ridge, seen also in *Eucalliax quadracuta* (Biffar, 1970).

Eucalliaxiopsis includes seven species from the Indo-West Pacific, of which three are newly described here, plus three species from the Western Atlantic: *E. cearaensis* (Rodrigues and Manning, 1992) from Brazil, *E. jonesi* from the Bahamas and *E. mcilhennyi* from Florida, USA. The species identified as *E.* HWI from Hawaii by Robles et al. (2020), which is genetically quite separate from six other species, was not available for study.

Eucalliaxiopsis panglaoensis, *E. dworschaki* and *E. paradoxa*, the last two being new species described here, differ from the others. All possess a transverse telson ridge beset with a row of short spiniform setae, a distally excavate uropodal endopod, a cheliped carpus with two distal spines on the upper margin, two mesiodistal lobes near the apex of the lower lateral margin plus a submarginal distal ridge on the mesial face. The carpus is similar to that of *Eucalliax quadracuta*, sole member of its genus. The first two of this group were found to be sister taxa by Robles et al. (2020) but the others were not monophyletic.

Calliaxiopsis Sakai and Türkay, 2014, was synonymised with *Calliaxina* by Poore and Dworschak (2017). *Bakercalliax* Sakai, 2018, *Heardcalliax* Sakai, 2018, and *Manningcalliax* Sakai, 2018, were all differentiated from *Eucalliax*, *Calliaxina* and from each other largely on the basis of the male pleopod 1 but also on the relative sizes of the appendices interna and masculina of pleopod 2. All were synonymised with *Eucalliaxiopsis* by Poore et al. (2019), who argued that similar forms of the male pleopod 1 are found in *Eucalliaxiopsis* and *Calliaxina* and that some of the forms used as generic characters by Sakai (2018) are characteristic of juveniles.

Key to Indo-West Pacific species of *Eucalliaxiopsis*

1. Telson with row of spiniform setae on transverse ridge; cheliped carpus with 2 short grooves perpendicular to distolateral margin near lower apex; uropodal endopod with apical concavity 2

– Telson without spiniform setae on transverse ridge; cheliped carpus distolateral margin smooth; uropodal endopod ovate 4

2. Cheliped carpus upper margin with proximal hook and subproximal submesial pit; cheliped propodus lateral face with longitudinal ridge extending from near carpus to base of finger; uropodal endopod with 8 short setae between apical clusters; widespread in Indo-West Pacific ..... *E. dworschaki* sp. nov.

– Cheliped carpus upper margin smooth; cheliped propodus lateral face with longitudinal ridge extending proximally slightly from base of finger; uropodal endopod with 10–11 short setae between apical clusters 3

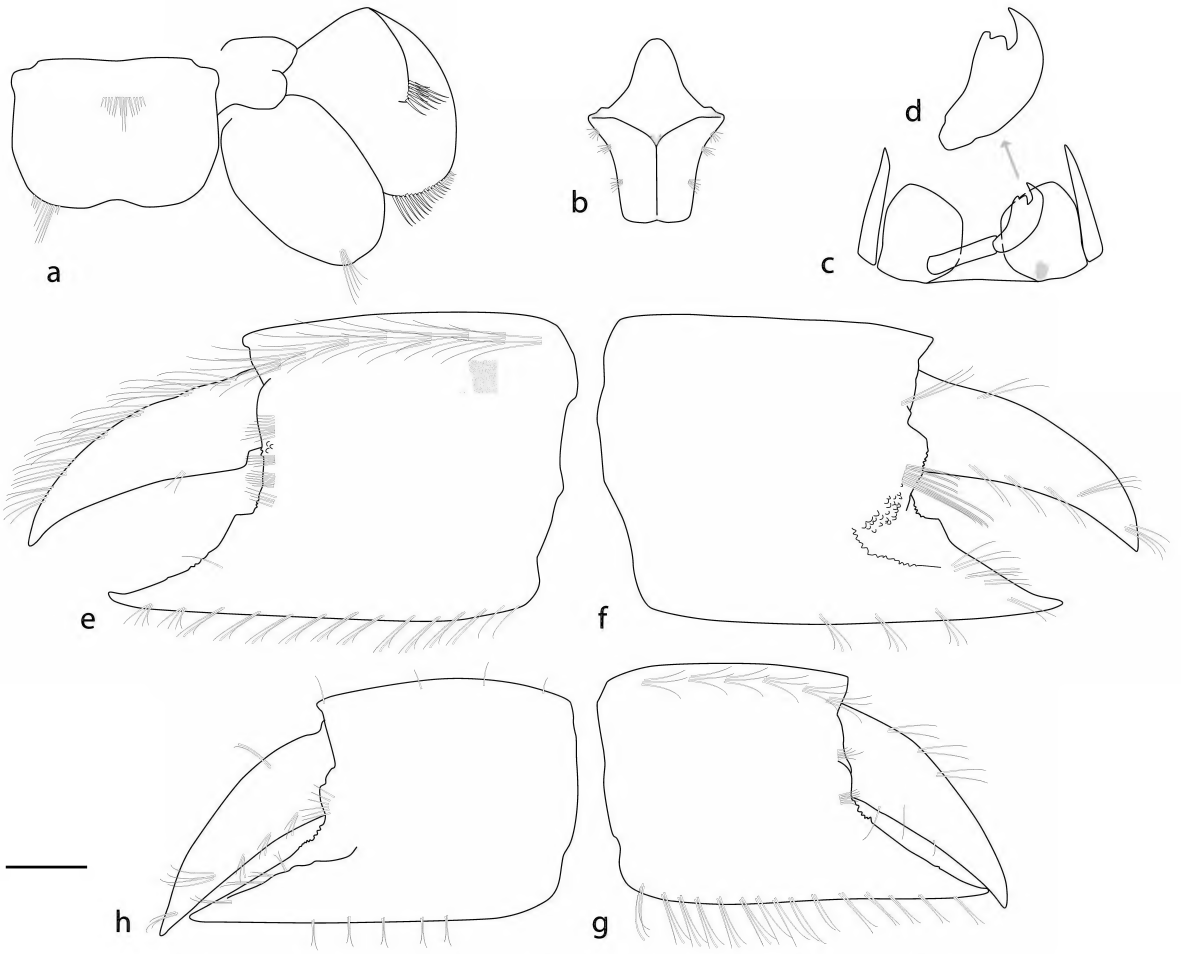

Figure 11. *Calliaxina sakaii*. Japan, NMV J59763 (male, 6.7 mm): a, telson, uropod; b, thoracic sternite 7; c, pleonal sternite 1 (anterior uppermost); d, pleopod 1; e, f, major cheliped propodus, dactylus (right), mesial, lateral views; g, h, minor cheliped propodus, dactylus (left), mesial, lateral views. Scale bars = 1 mm.

3. Chelipeds asymmetrical in male, major cheliped propodus longer than wide and longer than in female; distolateral lobe above lower margin of cheliped carpus with acute apex, ridged, oblique; Philippines, Japan ..... *E. panglaoensis* (Dworschak, 2006)

– Chelipeds similar in both sexes, major cheliped palm little longer than wide; distolateral lobe above lower margin of cheliped carpus with rounded apex, longitudinally grooved, perpendicular; NE Australia ..... *E. paradoxa* sp. nov.

4. Maxilliped 3 with exopod; cheliped merus lower margin with 2 denticles at midpoint, fixed finger with row of equally spaced setae along lateral ridge; telson with rounded posterior margin; female pleopod 2 with free extension beyond rami; Madagascar ..... *E. madagassa* (Sakai and Türkay, 2014)

– Maxilliped 3 without exopod; cheliped merus lower margin smooth, fixed finger with clusters of setae along lateral ridge; telson with truncate or excavate posterior margin; female pleopod 2 without extension beyond rami 5

5. Cheliped propodus upper mesial face with row of clusters of setae without associated transverse ridges; major cheliped of male upper margin as long as wide, similar to female; male pleopod 1 article 1 without distal setae, article 2 parallel-sided, apically rounded, with marginal setae, without appendix interna; S Australia ..... *E. aequimana* (Baker, 1907)

– Cheliped propodus upper mesial face with row of short transverse ridges associated with clusters of setae; major cheliped of male upper margin longer than wide, dissimilar to female; male pleopod 1 not as above 6

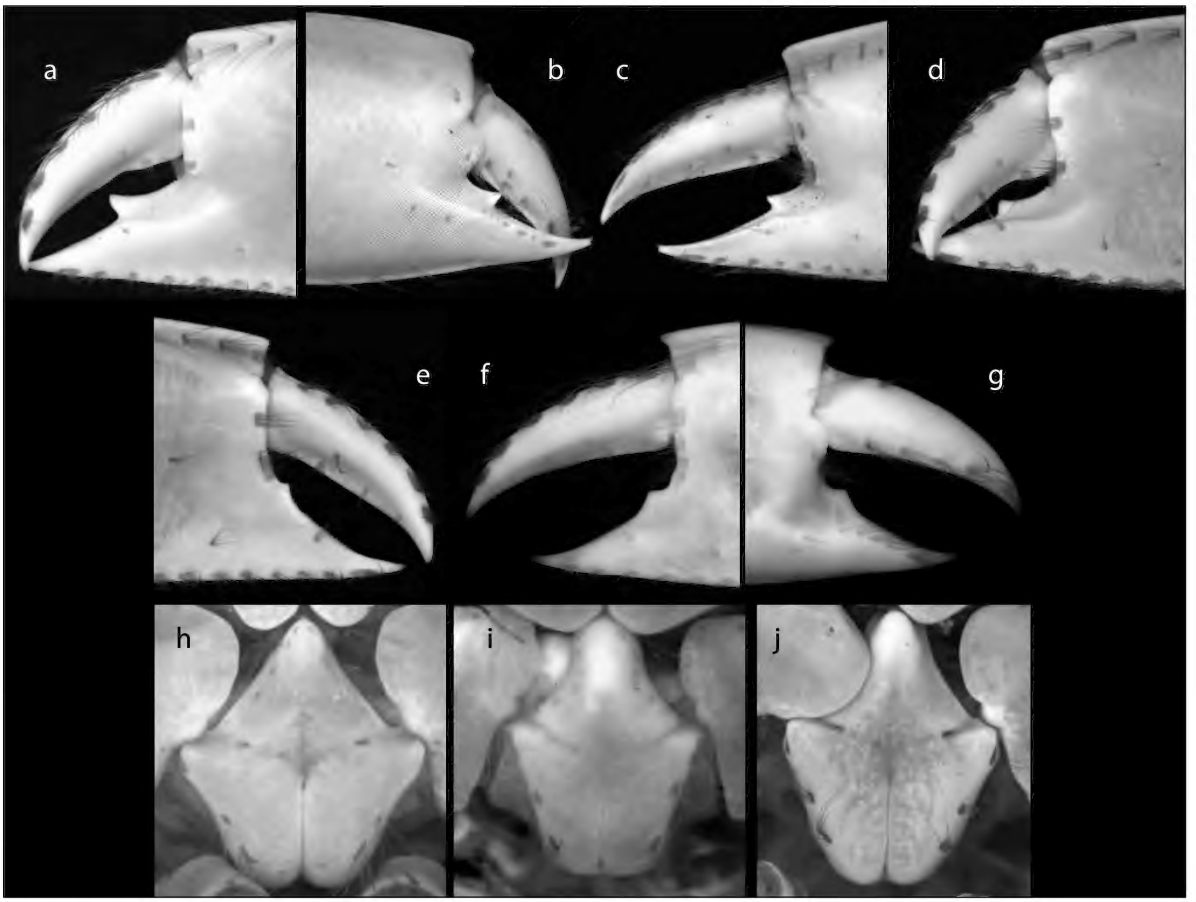

Figure 12. *Calliaxina* spp. *C. bulimba*: a, major cheliped, mesial. *C. kensleyi*: b, c, major cheliped lateral, mesial. *C. novaebritanniae*: d, major cheliped, mesial; e, minor cheliped, mesial. C. sakaii: f, g, minor cheliped mesial, lateral. Thoracic sterna: h, *C. bulimba*; i, *C. kensleyi*; j, *C. novaebritanniae*. Various scales.

6. Antenna peduncle 3 times as long as base of both eyes, most of article 5 exceeding antennule; telsonic ridge sharply elevated, with median notch; uropodal endopod 1.8 times as long as wide; female pleopod 2 without appendix interna; widespread in Indo-West Pacific ..... *E. inaequimana* (Dworschak, 2014)

– Antenna peduncle 2.4 times as long as base of both eyes, half of article 5 exceeding antennule; telsonic ridge slightly elevated, complete; uropodal endopod 1.5 times as long as wide; female pleopod 2 with appendix interna; Papua New Guinea ..... *E. patio* sp. nov.

Eucalliaxiopsis aequimana (Baker, 1907)

Figures 13, 14, 25a, b

Callianassa aequimana Baker, 1907: 182–185, pl. 24 figs 1–8.—Hale, 1927: 87, fig. 83.—Poore and Griffin, 1979: 245, figs 12, 13.

Callianassa (*Callichirus*) *aequimana*.—De Man, 1928b: 28, 93, 114.

Calliax aequimana.—de Saint Laurent and Manning, 1982: 222.—Sakai, 1988: 53, 61.— Sakai, 1999: 118–119 (not fig. 31).—Tudge et al., 2000: 145.—Davie, 2002: 459.—Sakai, 2005: 202.

Eucalliax aequimanus.—Poore, 2004: 184, fig.50e, f.

Calliaxina aequimana.—Sakai, 2011: 498–499.

Eucalliax aequimana.—Dworschak, 2014: 236, 244, figs 8, 9h, i.

Bakercalliax aequimana.—Sakai, 2018: 738.

Material examined. Australia. NSW, Balmoral Beach, 33.8° S, 151.3° E, AM P.3636 (male, 20 mm).

Victoria. San Remo, NW from rock outcrop 1.1 km E of Back Beach Rd (MRG transect 4), 38.53° S, 145.38° E, NMV J59759 (female, 9.6 mm). San Remo, channel bank end, 38.5233° S, 145.363° E, NMV J59762 (female, 6.6 mm). Port Phillip Bay, Geelong arm, 3 m, (NMV stn PPBES 953), 38.155° S, 144.545° E, NMV J16782 (4 females, 3.4–4.7 mm).

Tasmania. Waterhouse Island, 3–5 m, 40° 48' S, 147° 38.7' E (Moverley stn 52), NMV J71685 (juv., 2.9 mm). Georges Bay, Steiglitz Beach, 3–4 m, 41° 19.3' S, 148° 19.1' E (Moverley stn 42) NMV J71686 (juv., 2.9 mm).

South Australia. Port MacDonnell, 38.05° S, 140.7° E, NMV

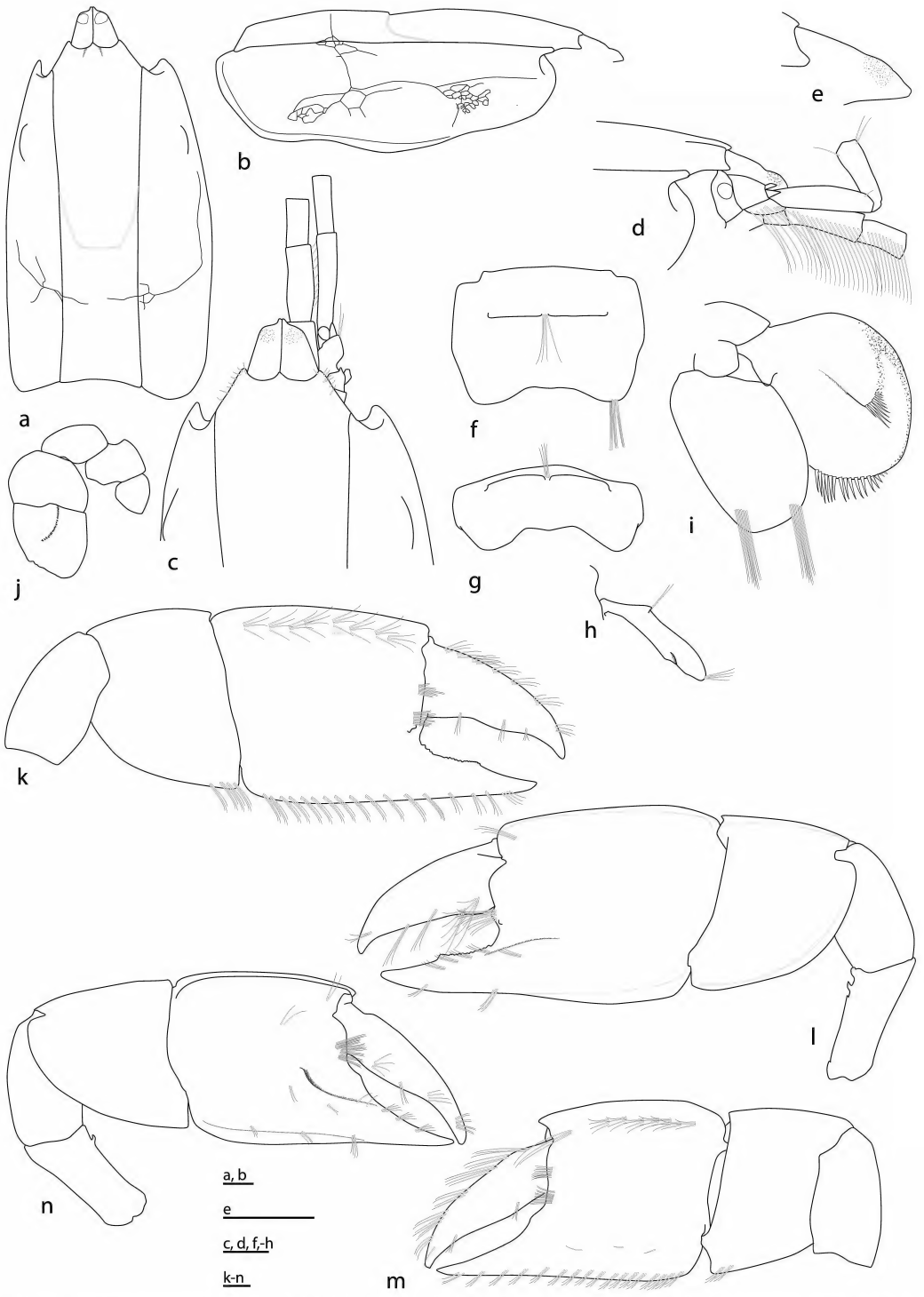

Figure 13. *Eucalliaxiopsis aequimana*. Australia, NMV J71687 (male, 11.0 mm): a, carapace, dorsal view; b, carapace, lateral view; c, d, anterior carapace, eyestalks, antennule, antenna, dorsal and lateral views; e, eyestalk, lateral view; f–h, telson, dorsal, postero-oblique, lateral views; i, right uropod; j, maxilliped 3; k, l, major cheliped (left), mesial and lateral views; m, n, minor cheliped (right), mesial and lateral views. Scale bars = 1 mm.

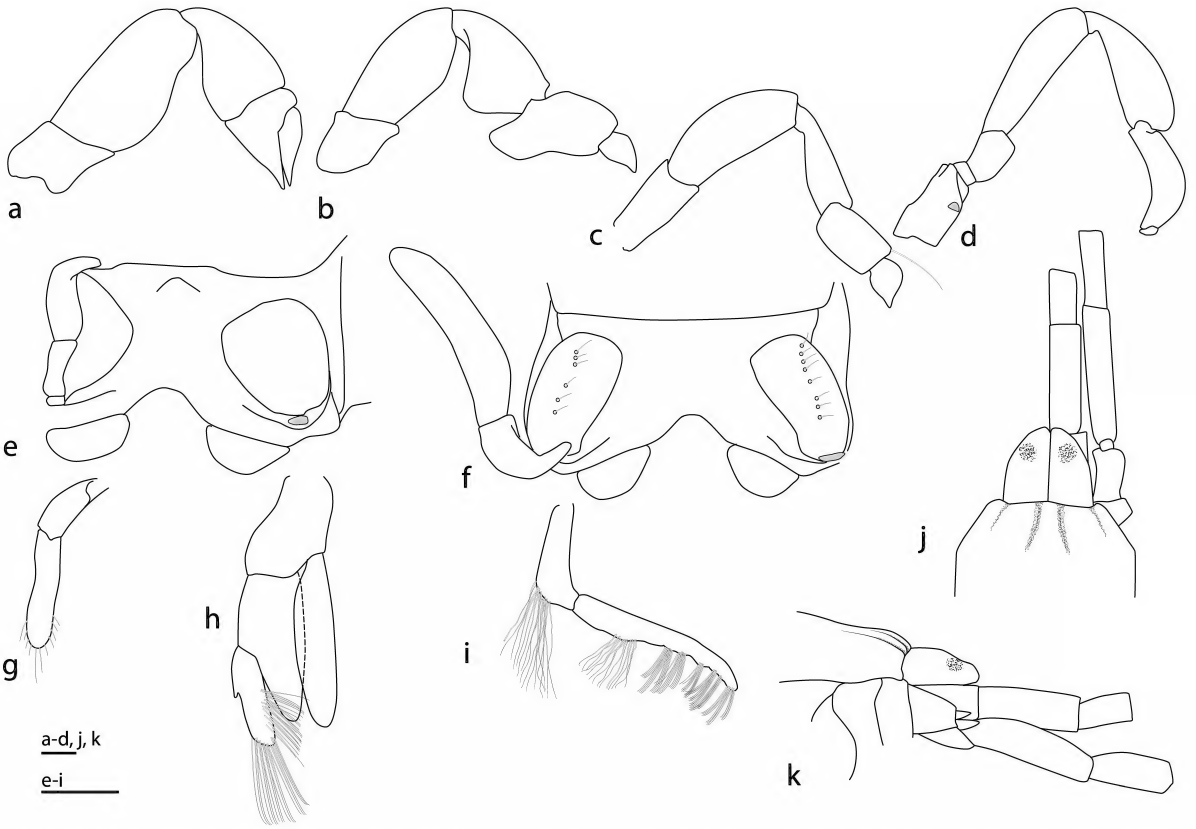

Figure 14. *Eucalliaxiopsis aequimana*. Australia, NMV J71687 (male, 11.0 mm): a, b, d, pereopods 2, 3, 5; e, pleonal sternite 1, right pleopod 1(anterior uppermost); g, h, left pleopods 1, 2, posterior views. NMV J759651 (female, 11.2 mm): c, pereopod 4; f, pleonal sternite 1, right pleopod 1; i, left pleopod 1, mesial view; j, k, anterior carapace, antennule, antenna, lateral and dorsal views. Scale bars = 1 mm.

J16783 (male, 12.8 mm). Dutton Bay, eastern shore, 34.0489° S, 136.415° E, NMV J71688 (male, 12.2 mm; 3 females, 8.9–11.9 MM), NMV J59651* (female, 11.2 mm). NMV J71687 (male, 11.0 mm).

Western Australia. Houtmans Abrolhos, WAM C9113 (male, 14.8 mm). Dalkeith, Swan River, WAM C1410 (male, 16.2 mm). Colpoy Point, Garden Island, 32° 12' S, 115° 40' E, WAM C11975 (female, 14.4 mm). Rockingham, Point Peron, Cockburn Sound, 32° 11' S, 115° 43' E, WAM C11973 (male, 12.9 mm). Fremantle Harbour, 32° 03' S, 115° 44' E, WAM C12030 (male, 20.3 mm). Mandurah, 32° 32' S, 115° 43' E, WAM C11978 (female, 15.8 mm). Bunbury, 33° 20' S, 115° 38' E, WAM C11990 (female, 10.1 mm). Harbour Board, Bunbury, WAM C5056 (female, 21.3 mm). Koombana Beach, Bunbury, 33° 20' S, 115° 38' E, WAM C12029 (male, 14.9 mm). Leschenault Estuary, Bunbury, 33° 20' S, 115° 38' E, WAM C11986 (male, 11.2 mm). Peel Inlet, 32° 36' S, 115° 43' E, WAM C11968 (male, 8.9 mm; female, 17.6 mm). Albany, 32° 00' S, 117° 52' E, WAM C11994 (female, 13.0 mm). Albany, WAM C6792 (female, 15.9 mm). Cheyne Beach, WAM C11987 (female, 19.8 mm). King George Sound, MNHN Th578 (female).

Diagnosis. Pleonite 1 with pleopods attached to pair of sternal plates. Eyestalk about twice as long as wide. *Antennule peduncle reaching to base of antenna peduncle article 5.* Maxilliped 3 exopod absent. Cheliped carpi distolateral margin square at lower angle, propodi lateral face with oblique longitudinal ridge extending from beyond mid-length of palm on to base of finger, upper mesial face with row of clusters of long setae. *Male pleopod 1 article 1 without distal setae, article 2 parallel-sided, apically rounded, with marginal setae, without appendix interna.* Female pleopod 2, appendix interna present. Uropod endopod ovate. Telson without transverse row of spiniform setae.

Description of male. Carapace smooth, with pair of shallow longitudinal groove posterior to rostrum; gastric–abdominal regions together 4.3 times as long as wide; branchiostegite calcified, with tessellated pattern of sulci; cervical groove at 0.6 carapace length, scarcely obvious on branchiostegite; cardiac sulcus at 0.76 carapace length, not meeting mid-dorsally, extending transversely across half of branchiostegite, with complex branches dorsally.

Rostrum blunt or obsolete. Anterolateral carapace lobe longer than rostrum, with rounded apex, anteriorly directed, with numerous submarginal dorsal setae.

Thoracic sternite 7 1.15 times as long as wide, with well-

defined median sulcus over posterior half, lateral groove anterior to coxal articulation poorly defined, oblique, not meeting medially, with 3 posterolateral clusters of long setae. Pleonal sternite 1with pair of swollen well marked areas anterior to ridge bearing pleopods; without setae. Pleonite 6 lateral margin smooth.

Eyestalks 1.6 times as long as wide at base, tapering around cornea, acute apical tubercle sometimes present; cornea subcircular. Antennular peduncle 2.5 times as long as width of both eyestalks; article 2 2.5 times as long as wide; article 3 0.6 times as long as article 2; articles 2 and 3 with ventrolateral row of long setae, continued onto flagellum. Antennal peduncle 3 times as long as width of both eyestalks, overreaching antennule peduncle by third of article 5; scaphocerite wider than long, subcircular; article 4 c. 5 times as long as wide; article 5 0.6 length of article 4. Maxilliped 3 ischium with slightly convex mesial margin, expanding from narrow proximomesial corner; ischium–merus upper margin 1.5 times as long as greatest width; crista dentata of c. 25 small teeth; carpus–dactylus together almost as long as ischium–merus.

Chelipeds subequal, propodus of major cheliped about 1.2 times that of minor, of similar widths, major dactylus stouter than that of minor. Major cheliped ischium twice as long as distal width, lower margin with short distal tooth; merus 1.8 times as long as broad, lower margin barely convex, unarmed; carpus 1.4 times as wide as upper length, upper margin carinate, distomesial and distolateral margins simple; propodus greatest width proximally, upper palm length 1.1 width, distomesial margin of palm with 2 submarginal groups each of c. 10 setae plus small submarginal bicuspid tooth, distolateral margin of palm with submarginal group of c. 10 setae between fingers plus small submarginal tooth; fixed finger half as long as upper margin of palm, cutting edge with microdenticles over proximal half, obsolete tooth at midpoint, with obsolete lateral ridge extending on to palm; dactylus overreaching fixed finger, 2.2 times as long as width at base, cutting edge sinuous; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers.

Minor cheliped ischium twice as long as distal width, lower margin with distal tooth; merus twice as long as broad, lower margin barely convex, unarmed; carpus 1.2 times as wide as upper length, upper margin carinate, distomesial and distolateral margins simple; propodus palm as wide as upper palm length, upper margin carinate, with blunt distal tooth, distomesial margin of palm with 2 submarginal groups of c. 10 and c. 12 setae, distolateral margin of palm with 2 submarginal groups of c. 8 and 10 setae; fixed finger half as long as upper margin of palm, cutting edge smooth, lateral concavity at base of fixed finger sharply defined by ridge on distal palm; dactylus barely overreaching fixed finger, 3.8 times as long as wide at base, cutting edge sinuous; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers.

Pereopod 2 merus twice as long as maximum width; dactylus 3 times as long as upper margin of propodus. Pereopod 3 merus twice as long as maximum width; carpus 1.6 times as long as wide; propodus with lower margin concave, 1.6 times as long overall as mid-length; dactylus half axial length of propodus. Pereopod 4 merus length 2.7 times maximum width; carpus 2.7 times as long as wide; propodus 1.5 times as long as wide, typically setose, with 1 long distal seta overlapping dactylus.

Pleopod 1 article 1 without distal setae; article 2 parallel-sided, apically rounded, 1.8 times as long as article 1, 4 times as long as wide, apex with c. 10 marginal setae, without appendix interna. Pleopod 2 endopod 2.4 times as long as wide; appendix masculina overreaching endopod by about fifth its length, setose along posterior face and distally; lobe-like appendix interna near midpoint of appendix masculina. Pleopod 3 with appendix interna submerged in endopod margin.

Uropodal endopod anterior margin convex, posterior margin almost straight, widest about third way along, 1.7 times as long as wide, apex broadly rounded, with 2 groups of long setae at ends of anterior and posterior margins; exopod ovate, all margins continuous, greatest dimension 1.3 times greatest width, with row of blade-like distal setae on distal margin; dorsal plate extending beyond half of exopod width, distal margin with spiniform setae. Telson 1.5 times as wide as long, broadest at midpoint, posterolateral corner rounded; posterior margin deeply excavate, with posterolateral cluster of long setae plus short spiniform seta; dorsal surface with sharp transverse ridge at anterior third, notched and with few long setae at midpoint.

Female. Essentially as male except: pleonal sternite 1 with pair of oval plates supporting pleopods, each with longitudinal row of 6–8 single setae emerging from pore. Pleopod 1 peduncle curved, with dense group of plumose setae; article 2 twice as long as article 1.

Distribution. Australia, NSW (as far north as 33° S), Tas., Vic., SA, WA (as far north as 25° S). Intertidal to subtidal sediments.

Remarks. Eucalliaxiopsis aequimana is recognised by the subequal chelipeds that are not sexually dimorphic. In a sample of 14 large specimens, the ratio between the upper propodus margins of major and minor chelipeds ranged from 1.1 to 1.3, with insignificant difference between males and females. The species is notable for the simple setose article 2 of the male pleopod 1, longer than article 1, lacking an appendix interna and acute apex.

The collection from Western Australia includes specimens with carapace lengths ranging 8.9–20.3 mm, most are larger than any from South Australia or Victoria, maximum cl. 12.8 mm. They differ most obviously in the near absence of a prominent rostrum (fig. 13j).

Sakai's (2005) synonymy includes references to other species from places outside southern Australia.

***Eucalliaxiopsis dworschaki* sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:E8BF2226-256F-4EF7-9DEB-DFD6955BB744

Figures 1f, g, 15–17, 25c–f

Eucalliax panglaoensis.—Dworschak, 2006: 356 (partim), fig. 5.—Kneer et al., 2013: 265.—Dworschak, 2018: 17 (partim; not fig. 1 = *E. panglaoensis*).

Calliaxina panglaoensis.—Sakai and Türkay, 2014: 191–192, fig. 12.

Eucalliaxiopsis aff. *panglaoensis.*— Robles et al., 2020.

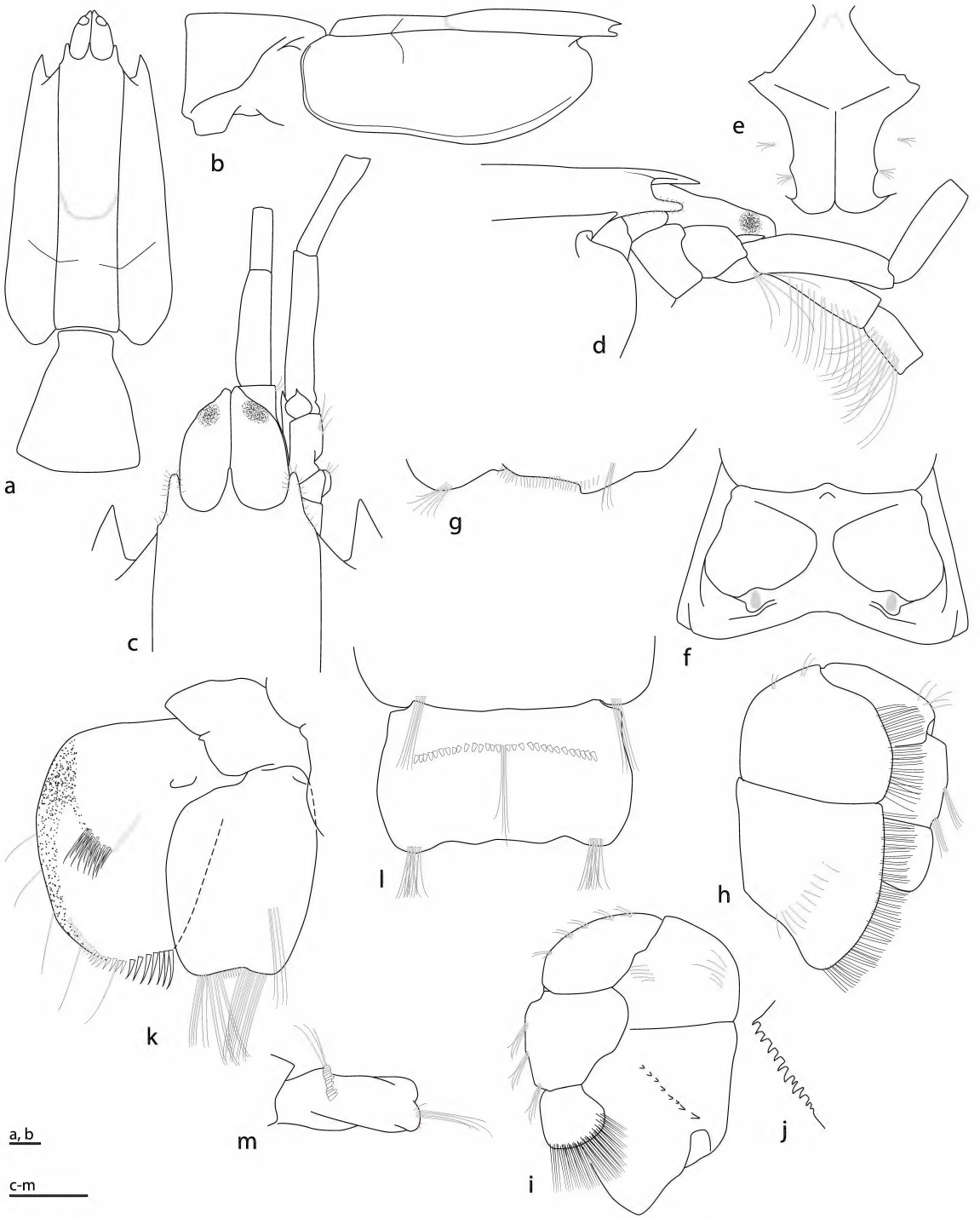

Figure 15. *Eucalliaxiopsis dworschaki* sp. nov. Holotype, MNHN-IU-2014-10003 (male, 8.9 mm): a, b, carapace, pleonite 1, dorsal and lateral views; c, d, anterior carapace, eyestalks, antennule, antenna, dorsal and lateral views; e, thoracic sternite 7; f, pleonite 1, sternite (anterior uppermost); g, pleonite 6, right lateral margin, oblique view; h, i, maxilliped 3; j, maxilliped 3, crista dentata; k, left uropod; l, m, telson, dorsal and lateral views. Scale bars = 1 mm.

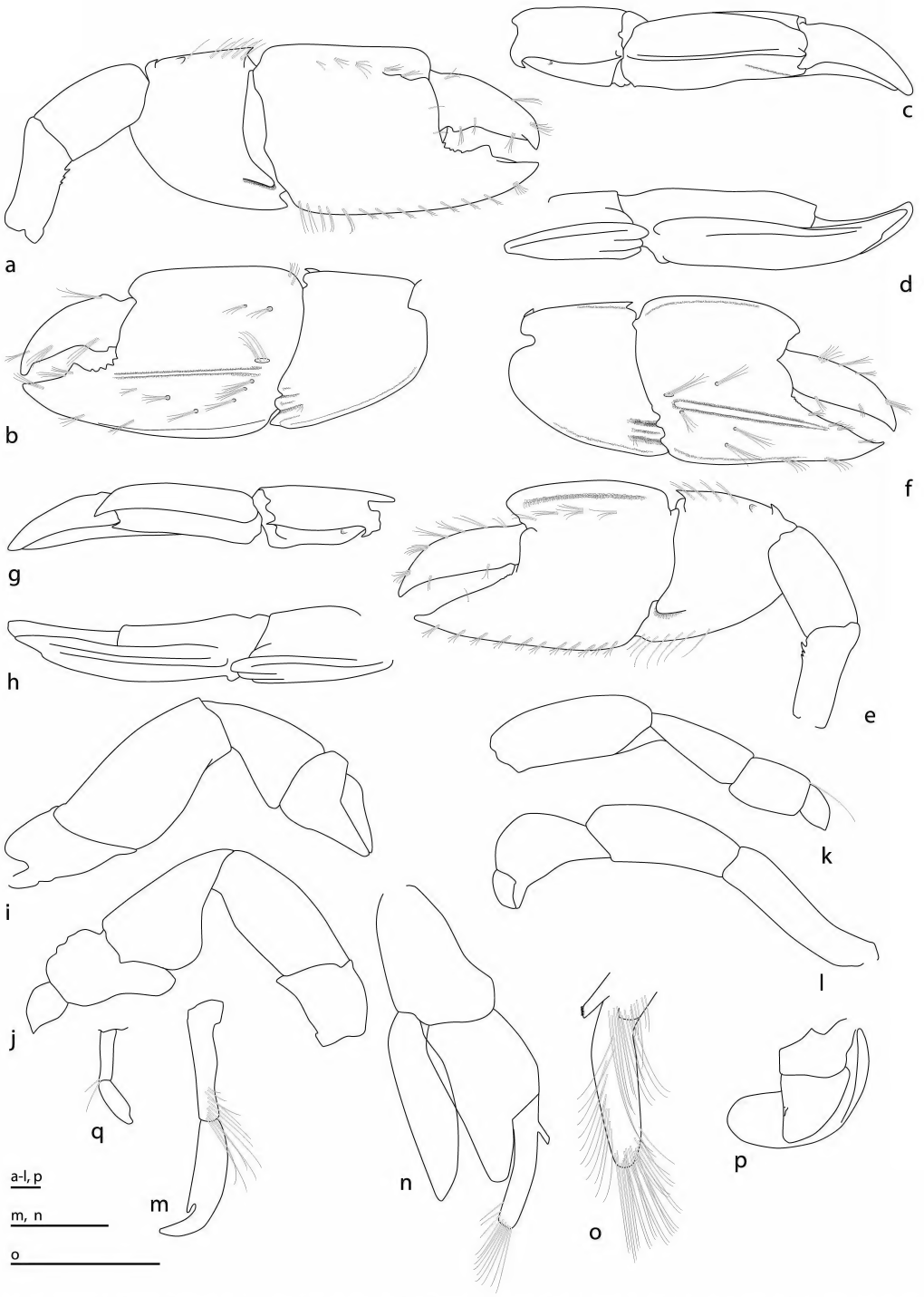

Figure 16. *Eucalliaxiopsis dworschaki* sp. nov. Holotype, MNHN-IU-2014-10003 (male, 8.9 mm): a, b, major cheliped (left), mesial and lateral views; c, d, major cheliped (left), carpus, propodus, dactylus, upper and lower views; e, f, minor cheliped (right), mesial and lateral views; g, h, minor cheliped (right), carpus, propodus, dactylus, upper and lower views; i–l, pereopods 2–5; m, right pleopod 1, mesial view; n, right pleopod 2, anterior view; o, appendices masculina, interna, posterior view; p, right pleopod 3, posterior view. UF 28877 (male, 6.0 mm): q, pleopod 1. Scale bars = 1 mm.

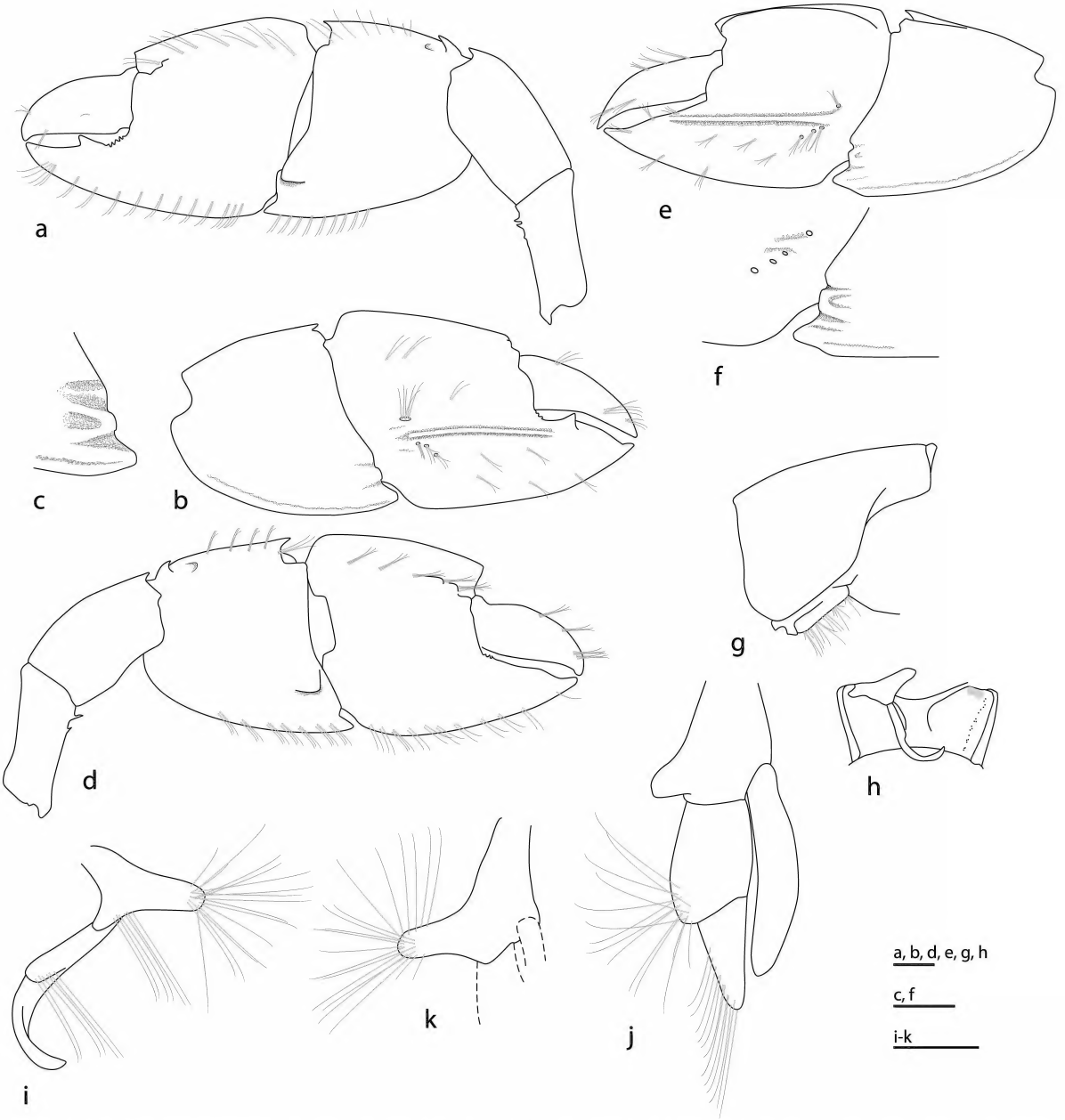

Figure 17. *Eucalliaxiopsis dworschaki* sp. nov. Paratype, MNHN-IU-2017-1351 (female, 8.2 mm): a, b, major cheliped (right), mesial and lateral views; c, carpus, lower distolateral margin, detail; d, e, minor cheliped (left), mesial and lateral views; f, carpus, lower distolateral margin, detail; g, pleonite 1; h, pleonal sternite 1, left pleopod 1 in situ (anterior uppermost); i, left pleopod 1, anterior view; j, k, left pleopod 2, posterior view, lateral view of peduncle. Scale bars = 1 mm.

Material examined. Holotype. Papua New Guinea, New Ireland, NW corner of Little Nusa Island, sand, 0–1 m, 02° 34.9' S, 150° 46.8' E (KAVIENG 2014 stn KM13), MNHN-IU-2014-10003* (male, 8.9 mm).

Paratypes. Papua New Guinea. Collected with holotype, MNHN-IU-2017-1351 (female, 8.2 mm). Madang Province, Riwo, mangrove, 05° 09' S, 145° 48.2' E, 1–2 m (PAPUA NIUGINI stn PR235), MNHN-IU-2013-7081 (female, 7.3 mm).

French Polynesia, Moorea, Papetoai, near 17.49° S, 149.88° W: stn BIZ-463, UF 28782* (female, 8.4 mm); stn BIZ-493, UF 28930 (female, 4.4 mm); stn BIZ-539, UF 28878* (male, 7.9 mm), UF 28877* (male, 6.0 mm); stn MIB-208, UF 16416 (female, 6.7 mm); stn MIB-195, UF 16286 (male, 8.8 mm); stn MIB-227, UF 16531 (male, 5.4 mm). Off Nihimaru River estuary, 17.533° S, 149.9045° W, stn MIB-098, UF 15946 (male, 2.9 mm).

Other material. Australia, Qld, Great Barrier Reef, Myrmidon Reef, 18.27° S, 147.38° E, October 1986: lagoon with "*Callianassa*" mounds, 4 m, (M. Riddle stn M/10/2), NMV J71681 (male, 8.4 mm); 8 m, (M. Riddle stn M/10), NMV J71682 (female, 9.2 mm).

Marianas Island, W coast of Guam, near Fisheye Marine Park, seagrass bed, 0.2–0.5 m (stn AA05), UF GUOK 10-0378, (male, 3.7 mm).

Madagascar, Toliara (as Tuléar), Thomassin stn 678, MNHN-IU-2016-8083 (female, 8.9 mm).

Diagnosis. Pleonite 1 with pleopods attached to pair of sternal plates. Eyestalk about twice as long as wide. Antennule peduncle reaching to midpoint of antenna peduncle article 5. Maxilliped 3 exopod absent. *Cheliped carpi distolateral margin with 3 rounded lobes near lower margin separated by submarginal grooves parallel to lower margin, second lobe with slight median depression*, propodi lateral face with horizontal longitudinal ridge extending from near carpus to base of finger, upper mesial face with row of clusters of long setae. Male pleopod 1 article 1 linear, with distal setae; article 2 blade-like with subapical medial notch. Female pleopod 2, appendix interna absent. Uropod endopod ovate with excavate apex. Telson with row of spiniform setae on ridge.

Description of holotype male. Carapace length 8.9 mm, smooth; gastric–abdominal regions together 4.7 times as long as wide; branchiostegite fully calcified; cervical groove at 0.60 carapace length, scarcely obvious on branchiostegite; cardiac sulcus at 0.77 carapace length, not meeting mid-dorsally, extending transversely across third of branchiostegite.

Rostrum acute, tapering to narrow tip, length about 0.4 width of eyestalks. Anterolateral carapace lobe almost as long as rostrum, with rounded apex, anteriorly directed, with numerous submarginal dorsal setae.

Thoracic sternite 7 1.2 times as long as wide, with well-defined median sulcus over posterior half, lateral groove anterior to coxal articulation well defined, oblique, meeting medially, with 3 posterolateral clusters of long setae. Pleonal sternite 1 with pair of swollen relatively unchitinised areas anterior to ridge bearing pleopods; without setae. Pleonite 6 with small lateral blunt hook-like process at midpoint.

Eyestalks twice as long as wide at base, tapering to cornea and acute apical tubercle; cornea subcircular. Antennular peduncle 3 times as long as width of both eyestalks; article 2 3.5 times as long as wide; article 3 half as long as article 2; articles 2 and 3 with ventrolateral row of long setae, continued onto flagellum. Antennal peduncle 3.4 times as long as width of both eyestalks, overreaching antennule peduncle by most of article 5; scaphocerite wider than long, with acute apex; article 4 c. 5 times as long as wide; article 5 0.65 length of article 4. Maxilliped 3 ischium with slightly convex mesial margin, expanding from narrow proximomesial corner; ischium–merus upper margin 1.6 times as long as greatest width; crista dentata of 12 spines, the most proximal reflexed; carpus–dactylus together almost as long as ischium–merus.

Chelipeds unequal, of similar lengths, propodi of similar widths, major dactylus stouter than that of minor. Major cheliped (left in holotype) ischium twice as long as distal width, lower margin with short spines becoming more distinct distally; merus 1.8 times as long as broad, lower margin mostly straight, unarmed; carpus 1.4 times as wide as upper length, upper margin carinate, with proximal hooked tooth, subproximal mesial pit, distal tooth, distomesial margin with prominent lobe near lower margin, distomesial face with lower submarginal ridge, distolateral margin with rounded notch near upper margin, with 3 rounded lobes near lower margin separated by submarginal grooves parallel to lower margin, second lobe with slight median depression, 2 short setae in lower groove; propodus greatest width in middle of palm, upper palm length equal to greatest width, upper margin carinate, with rounded lobe projecting over dactylus, lower margin carinate, strongly curved mesially, mesial face with short distal uneven setose ridge below upper margin, distomesial margin of palm almost straight, lateral face of palm with prominent ridge running from tubercle near proximal margin on to finger, oblique row of tubercles at proximal end of ridge, each perforated for cluster of setae; fixed finger half length of upper margin of palm, cutting edge with denticles over proximal half, blunt triangular tooth at about midpoint; dactylus as long as fixed finger, twice as long as wide at base, cutting edge with blunt molar, with deflected tip; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers.

Minor cheliped (right in holotype) ischium twice as long as distal width, lower margin with distal spine; merus 1.7 times as long as broad, lower margin mostly straight, unarmed; carpus 1.4 times as wide as upper length, upper margin carinate, with proximal hooked tooth, subproximal mesial pit, distal tooth, distomesial face with lower submarginal ridge, distolateral margin with notch near upper margin, with 3 lobes near lower margin separated by perpendicular submarginal grooves, middle lobe apex rounded, with shallow median groove, 3 short setae in lower groove; propodus greatest width in middle of palm, upper palm length equal to greatest width, as wide distally as proximally, upper margin carinate, overhanging mesial face, with rounded lobe projecting over dactylus, lower margin carinate, strongly curved mesially, distomesial margin of palm almost straight, lateral face of palm with prominent ridge running from tubercle near proximal margin on to finger, oblique row of tubercles at proximal end of ridge, each perforated for cluster of setae; fixed finger 0.7 length of upper margin of palm, width at base half width of palm, cutting edge smooth; dactylus as long as fixed finger, 3.5 times as long as wide at base, cutting edge straight; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers.

Pereopod 2 merus twice as long as maximum width; dactylus c. 2.5 times as long as upper margin of propodus. Pereopod 3 merus 2.2 times as long as maximum width; carpus 1.8 times as long as wide; propodus with lower margin concave, 1.5 times as long overall as mid-length; dactylus 0.7 times length of axial length of propodus. Pereopod 4 merus length 2.7 times maximum width; carpus 2.7 times as long as wide; propodus 1.5 times as long as wide, typically setose, with 1 long distal seta overlapping dactylus.

Pleopod 1 article 1 distally setose; article 2 as long as article 1, 4 times as long as wide, with apex curved over subdistal notch, appendix interna freely produced, unarmed. Pleopod 2 endopod 2.1 times as long as wide; appendix masculina overreaching endopod by about half its length, setose along posterior face and distally; appendix interna near base of appendix masculina with 5 small hooks. Pleopod 3 with appendix interna submerged in endopod margin.

Uropodal endopod anterior margin convex, posterior margin convex, widest about third way along, 1.4 times as long as wide, apex excavate, with rows of long setae at ends of anterior and posterior margins, with 11 short setae between in excavation, with subdistal group of facial setae; exopod ovate, anterior margin straight, distal and posterior margins continuous, greatest dimension 2.3 times anterior margin, with row of blade-like distal setae on distal margin, c. 6 not overlapping with densely setose distal margin; dorsal plate extending almost half of exopod width, distal margin with spiniform setae. Telson 1.8 times as wide as long, broadest at midpoint, posterolateral corner squarish; posterior margin sinuous, lateral regions most prominent, with posterolateral cluster of long setae plus 2 short spiniform setae; dorsal surface with sharp transverse ridge at anterior third, with 30 short spiniform setae, few long setae at midpoint.

Female. Essentially as male except: major cheliped palm more tapering than in male, widest proximally. Pleonal sternite 1with pair of oval plates supporting pleopods, each with longitudinal row of c. 20 setae in clusters of 4 or 5. Pleopod 1 peduncle with mesial setose lobe longer than base. Pleopod 2 peduncle with similar lobe directed mesially.

Colour. Exoskeleton mostly translucent white, upper parts of chelipeds pink (fig. 1f, g).

Etymology. For Peter C. Dworschak, good friend and colleague, and in recognition of his career devoted to the biology of "thalassinideans".

Distribution. Madagascar, Philippines, Mariana Islands, Papua New Guinea, Indonesia, French Polynesia. Intertidal to 8 m.

Remarks. *Eucalliaxiopsis dworschaki* is similar to *E. panglaoensis* and *E. paradoxa* (see remarks under *Eucalliaxiopsis* above). *Eucalliaxiopsis dworschaki* differs from both species in possession of a proximal hooked spine and subproximal-mesial pit on the upper margin of the carpus of both chelipeds (figs 16g, 25d, e) and a lateral ridge extending almost the entire length of the propodus of both chelipeds (figs 16b, 25b). The palm of the major cheliped of the male is a little longer than wide, while it is 1.25 times as long as wide in *E. panglaoensis*. The telson is relatively shorter (length: width ratio 1.8 vs 1.6) and with a more sinuous posterior margin, and the uropodal endopod is broader (length: width ratio 1.4 vs 1.6). Dworschak (2006; pers. comm. 29 September 2019) reported a small spine on the merus of maxilliped 3 of the allotype of *E. panglaoensis*, and of seven from Sulawesi, here reidentified as *E. dworschaki*. None of the material examined for this study, nor Dworschak's two individuals from Bali, possess this spine. *Eucalliaxiopsis paradoxa* is compared below.

Dworschak (2006: 356, fig. 5) remarked on and illustrated two females from Panglao that differed from typical *E. panglaoensis*. He noted the hook and pit on the upper margin of the cheliped carpus and the longitudinal ridge on the propodus, characters used here to differentiate *E. dworschaki*. The genetic difference from *E. panglaoensis* from the type locality in the Philippines (Robles et al., 2020) and consistent morphology of *E. dworschaki* over a wide geographic range in the Indo-West Pacific support recognition of two species. Dworschak (2018) listed material of *E. panglaoensis* from Sulawesi and Bali, Indonesia. He has now confirmed (pers. comm. 30 October 2018) that this collection of five males and four females also belongs to *E. dworschaki*. The two species occur sympatrically at Panglao and a single individual of *E. dworschaki* was recorded from Guam, not far from the Philippines. A large sample of ghost shrimps from the Great Barrier Reef, a sample that included specimens of *Corallianassa* sp. (Callichiridae) and *Thomassinia aimsae* Poore, 1997 (Callianideidae), was dominated by *E. paradoxa* but also included one specimen of *E. dworschaki*.

There is no genetic difference between the individual from Papua New Guinea and the three sequenced from French Polynesia.

Sakai and Türkay (2014) illustrated a single somewhat distorted individual from Papua New Guinea that was identified as *Calliaxina panglaoensis*. On the basis of its recorded locality, the specimen is probably *E. dworschaki*.

Eucalliaxiopsis inaequimana Dworschak, 2014

Figures 1h, i, 18, 25h

Callianassa aequimana.—Poore and Griffin, 1979: 245 (partim from Qld).

Calliax aequimana.—Sakai, 1999: 118–119 (partim from Maldives), fig. 31.

Eucalliax inaequimana Dworschak, 2014: 236–244, figs 3–7, 9f, g, 10e, f.—Dworschak, 2018: 17.

Eucalliaxiopsis inaequimana.—Poore et al., 2019: 125, 127, fig. 19o, p.—Robles et al., 2020.

Material examined. Papua New Guinea, New Ireland, NW corner of Little Nusa Island, seagrass, 0–1 m, 02° 34.9' S, 150° 46.4' E (KAVIENG 2014 stn KM11), MNHN-IU-2013-10006* (female, 5.8 mm), MNHN-IU-2013-10008* (male, 7.2 mm).

Australia. Qld. Great Barrier Reef, Myrmidon Reef, 18.27° S, 147.38° E, October 1986, 4 m (M. Riddle stn M/10/2), NMV J71689 (2 males, 7.1 mm; 5 females, 5.3–8.3 mm); 2 m (M. Riddle stn M/10/3), NMV J71690 (female, 5.6 mm). Norwest Islet, Capricorn Group, 23.3° S, 151.7° E, AM P.10356 (male, 8.1 mm)

Mariana Islands, Guam, W coast, near Fish Eye Marine Park,

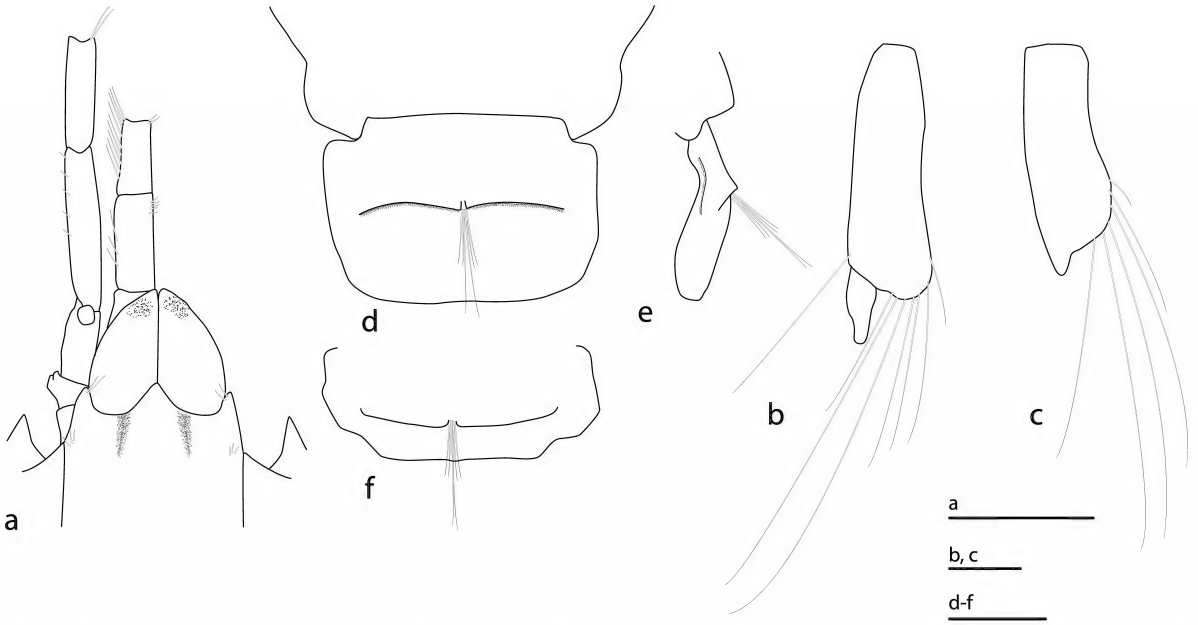

Figure 18. *Eucalliaxiopsis inaequimana*. French Polynesia, UF 16512 (male, 5.0 mm): a, anterior carapace, eyestalks, antennule, antenna; b, pleopod 1. French Polynesia, UF 28903 (male, 5.4 mm): c, pleopod 1. Papua New Guinea, MNHN-IU-2014-10008 (male, 7.2 mm): d–f, telson, dorsal, lateral and anterodorsal views. Scale bars a, d–f = 1 mm; scale bars b, c = 0.1 mm.

sand/rubble flat, 0.2–0.5 m, 13.471° N, 144.704° E (stn AA05), UF 27330 (female, 3.5 mm).

French Polynesia. Moorea Island, Motu Tiahura/Fareone channel, 17.4888° S, 149.9134° W (stn MIB-225), UF 16512 (male, 5.0 mm). Papetoai, 17.4898°S, 149.884°W, (stn BIZ-463), UF 16479 (female, 3.9 mm), UF 28784* (male, 5.1 mm); stn BIZ-493 UF 28903 (male, 5.4 mm), UF 28929 (female, 5.1 mm). S of Nihimaru, 17.535° S, 149.904° W (stn BIZ-616), UF 29162 (ovigerous female, 6.6 mm). Off Opunohu public beach, 17.49143° S, 149.85138° W (stn BIZ-636), UF 29208 (male, 6.0 mm). Off Nihimaru river estuary, 17.533° S, 149.9045° W (stn MIB-098), UF 15915 (male, 5.0 mm), UF 15945 (female, 4.0 mm). Gump reef, in front of waterfront bungalows, 17.4902° S, 149.826° W (stn MIB-224), UF 16498 (ovigerous female, 6.2 mm). Between Papetoai and Hotel, 17.4908° S, 149.8871° W (MIB-227), UF 16535 (male, 2.9 mm), UF 16542 (female, 4.6 mm; male, 4.1 mm).

Diagnosis. Pleonite 1 without pair of sternal plates. *Eyestalk about twice as long as wide*. Antennule peduncle reaching to base of antenna peduncle article 5. Maxilliped 3 exopod absent. Cheliped carpi distolateral margin square at lower angle, propodi lateral face without longitudinal ridge, *upper mesial face with row of short transverse ridges associated with more distal clusters of setae*. Male pleopod 1 article 1 linear, with distal setae; article 2 short, oblique, or of single article with narrower distal lobe. Female pleopod 2, appendix interna absent. Uropod endopod ovate. Telson without transverse row of spiniform setae.

Colour. Exoskeleton mostly translucent white, gastric region, distal propodus of chelipeds with few pink chromatophores (fig. 1h, i).

Distribution. Australia, Cocos (Keeling) Island (type locality), Qld, Great Barrier Reef; Papua New Guinea, New Ireland; Indonesia, Sulawesi; Philippines, Panglao; French Polynesia. Intertidal to 4 m.

Remarks. Dworschak (2014) distinguished this species, as *Eucalliax inaequimana*, on several features including inequality of the chelipeds in both sexes from *E. aequimana*. Usually, only males of *Eucalliaxiopsis* have a significantly larger major cheliped although not all descriptions are clear on this point. The same is true of *E. patio* (described and compared below) and both species differ from *E. aequimana* in the ways listed by Dworschak (2014).

Robles et al.'s (2020) phylogram detected no genetic difference between two individuals from the type locality, two from Papua New Guinea and one from French Polynesia. Dworschak (2014) recorded the maximum carapace length as 9.1 mm; the largest in this collection were a male of 7.2 mm and ovigerous female of 6.2 mm. His illustrations and description were comprehensive, and many specific details appear on the new material, such as the transverse ridges on the mesial faces of the chelipeds and distal tubercles on the cheliped propodus. A broad postrostral obsolete median ridge defined by shallow longitudinal grooves is typical of the new material (fig. 18a) but was not mentioned by Dworschak (2014). The feature appears to be more conspicuous in some individuals than others (Dworschak, pers. comm. 29 September 2019). The male pleopod 1 is manifest in two forms – a long article and shorter second article (fig. 18b; as

figured by Dworschak) – and a form where these appear fused (fig. 18c).

Poore and Griffin's (1979) specimen of *Callianassa aequimana* from Queensland was reidentified as *E. inaequimana*. Sakai's (1999) record of *Calliax aequimana* from the Maldives is almost certainly referable to *E. inaequimana*. Sakai (2018) omitted *E. inaequimana* from his revision of Eucalliacinae.

Eucalliaxiopsis madagassa (Sakai and Türkay, 2014)

Figure 19

Calliaxiopsis madagassa Sakai and Türkay, 2014: 193, fig. 13.
Calliaxina thomassini Ngoc-Ho, 2014: 549, fig. 2.
Calliaxina madagassa.—Poore and Dworschak, 2017: 120, fig. 1.

Material examined. Madagascar. Nosy Bé, W of Hell-Ville, 13.41562° S, 48.24648° E (stn MGNW-50), UF 14090 (ovigerous female, 5.8 mm). Toliara (as Tuléar), Thomassin stn 676, MNHN-IU-2016-8085 (ovigerous female, 5.8 mm).

Diagnosis. Eyestalk about twice as long as wide. Antennule peduncle reaching to midpoint of antenna peduncle article 5. *Maxilliped 3 exopod present.* Cheliped carpi distolateral margin square at lower angle, propodi lateral face without longitudinal ridge, upper mesial face with row of clusters of long setae. Male pleopod 1 article 1 without distal setae, article 2 parallel-sided, apically rounded, with marginal setae, without appendix interna. Female pleopod 2, appendix interna absent. Uropod endopod ovate. Telson without transverse row of spiniform setae.

Distribution. Madagascar.

Remarks. Poore and Dworschak (2017) discussed the synonymy and priority of the species names before *Calliaxina* was divided into two by Poore et al. (2019). The species is widespread in Madagascar (Ngoc-Ho, 2014) and is recognised by rounded posterolateral corners and convex posterior margin of the telson, the continuous dense row of setae on the lateral margin of the fixed finger of the minor cheliped, and the presence (usually) of two or three tubercles at the midpoint of the lower margin of the cheliped merus. The ovigerous female differs from that of the male figured by Ngoc-Ho (2014) in having a slightly narrower uropodal exopod and in having the chelipeds subequal – they are unequal in males of most species of this genus.

Eucalliaxiopsis panglaoensis (Dworschak, 2006)

Figure 25g

Eucalliax panglaoensis Dworschak, 2006: 349–358, figs 1–4, 6, 7 (not fig. 5 = *E. dworschaki* sp. nov.).—Osawa and Fujita, 2016: 40–41, fig. 3c.—Dworschak, 2018: 17, fig. 1 (partim).
Calliaxina panglaoensis.—Sakai, 2011: 501.
Eucalliaxiopsis panglaoensis.—Poore et al., 2019: 125, 127, 146, fig. 19m.—Robles et al., 2020.

Material examined. Paratypes. Philippines, Panglao Island, 09° 38.3' S, 123° 49.6' E, MNHN Th1503 (female, 7.1 mm), MNHN Th1504 (male, 4.3 mm).

Diagnosis. Pleonite 1 with pleopods attached to pair of sternal plates. Eyestalk about twice as long as wide. Antennule peduncle reaching to midpoint of antenna peduncle article 5. Maxilliped 3 exopod absent. *Cheliped carpi distolateral margin with 3 acute teeth near lower margin separated by wide grooves parallel to lower margin, second tooth with acute ridge*, propodi lateral face without longitudinal ridge, upper mesial face with row of clusters of long setae. Male pleopod 1 article 1 linear, with distal setae; article 2 blade-like with subapical medial notch. Female pleopod 2, appendix interna absent. Uropod endopod ovate with excavate apex. Telson with row of spiniform setae on ridge.

Distribution. Philippines, Panglao; Japan, Ryukus, Miyako Group. Sandy beaches, intertidal to 4 m.

Remarks. *Eucalliaxiopsis panglaoensis* differs from *E. paradoxa* and *E. dworschaki* (see remarks under *Eucalliaxiopsis* above and these two species) in armature of the cheliped. The marginal teeth at the lower distal angle of the carpus are more widely spaced, and the second more sharply ridged than in the other two. The longitudinal lateral ridge on the propodus is shorter than in *E. dworschaki* but more prominent than in *E. paradoxa* (fig. 25g; Dworschak, 2006).

The record of this species, rather than *E. dworschaki*, from Japan is based on the illustration of the cheliped with a short lateral propodal ridge (Osawa and Fujita, 2016: fig. 3c).

Eucalliaxiopsis paradoxa sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:2EEAC4EC-C3EA-4D17-9102-4090CA6DF02E

Figures 20, 21, 25h, i

Material examined. Holotype. Australia, Qld, Great Barrier Reef, Rib Reef, 18.48° S, 146.86° E, October 1985, shallow lagoon, 4 m, (M. Riddle stn R/10/2), NMV J71683 (male, 9.4 mm).

Paratypes. Collected with holotype. NMV J71679 (ovigerous female, 9.4 mm), NMV J71684 (3 females, 9.8–10.9 mm). Australia, Qld, Great Barrier Reef, Myrmidon Reef, 18.27° S, 147.38° E, October 1985, lagoon with "*Callianassa*" mounds, 8 m, (M. Riddle stn M/10/1), NMV J71680 (7 males, 3.9–10.3 mm; 7 females, 4.4–10.4 mm).

Diagnosis. Pleonite 1 with pleopods attached to pair of sternal plates. Eyestalk about twice as long as wide. Antennule peduncle reaching to midpoint of antenna peduncle article 5. Maxilliped 3 exopod absent. *Cheliped carpi distolateral margin with 3 acute teeth near lower margin separated by submarginal oblique grooves, second tooth with prominent rounded ridge*, propodi lateral face with short horizontal longitudinal ridge extending from beyond mid-length of palm to base of finger, upper mesial face with row of clusters of long setae. Male pleopod 1 article 1 linear, with distal setae; article 2 blade-like with subapical medial notch. Female pleopod 2, appendix interna absent. Uropod endopod ovate with excavate apex. Telson with row of spiniform setae on ridge.

Description of holotype male. Carapace length 9.4 mm, smooth; gastric–abdominal regions together 4.7 times as long as wide; branchiostegite fully calcified; cervical groove at 0.63 carapace length, scarcely obvious on branchiostegite; cardiac sulcus at 0.8 carapace length, not meeting mid-dorsally, extending transversely across quarter of branchiostegite.

Rostrum acute, tapering evenly over most of length, length 0.5 width of eyestalks. Anterolateral carapace lobe 0.6 length

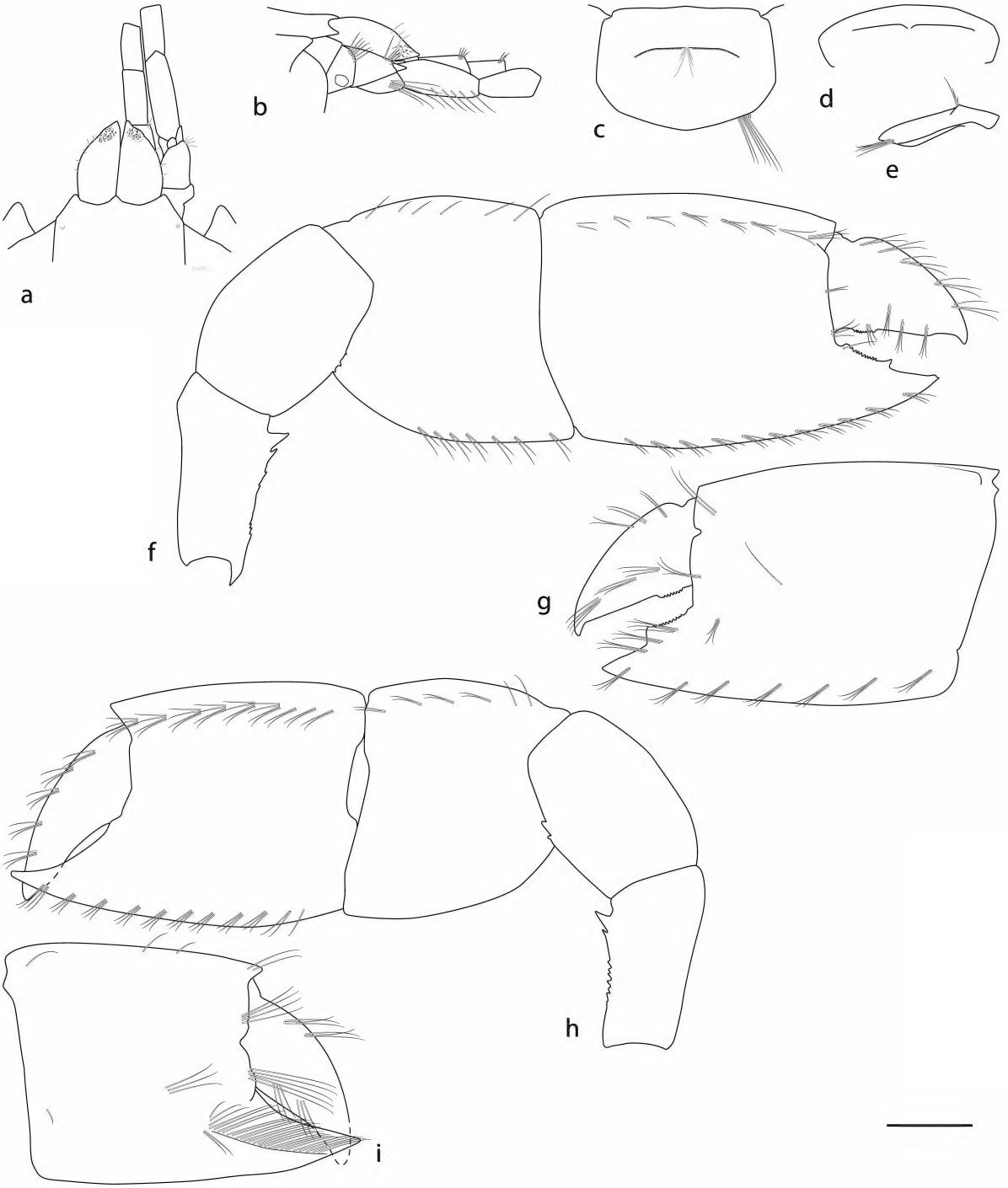

Figure 19. *Eucalliaxiopsis madagassa*. Madagascar, UF 14090 (ovigerous female, 5.8 mm): a, b, anterior carapace, eyestalks, antennule, antenna, dorsal and lateral views; c–e, telson, dorsal, posterior and lateral views; f, major (left) cheliped, mesial view; g, major (left) cheliped, propodus, dactylus, lateral view; h, minor (right) cheliped, mesial view; i, minor (right) cheliped, propodus, dactylus, lateral view. Scale bars = 1 mm.

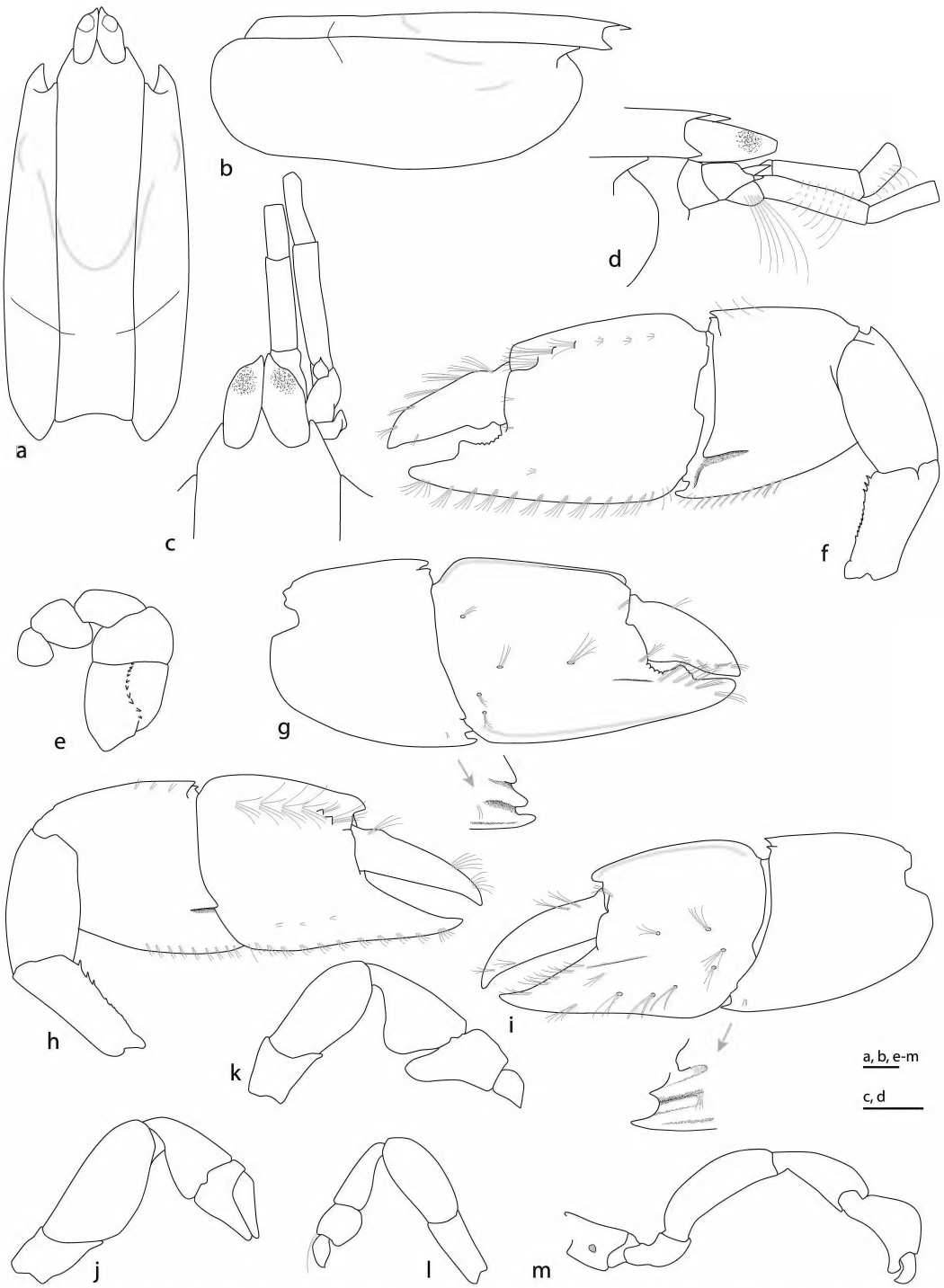

Figure 20. *Eucalliaxiopsis paradoxa* sp. nov. Holotype, NMV J71683 (male, 9.4 mm): a, b, carapace, dorsal and lateral views; c, d, anterior carapace, eyestalks, antennule, antenna, dorsal and lateral views; e, maxilliped 3; f, g, major cheliped (left), mesial and lateral views, with detail of distolateral corner of carpus; h, i, minor cheliped (right), mesial and lateral views, with detail of distolateral corner of carpus; j, k, m, pereopods 2, 3, 5. Paratype, NMV J71680 (female, 9.3 mm): l, pereopod 4. Scale bars = 1 mm.

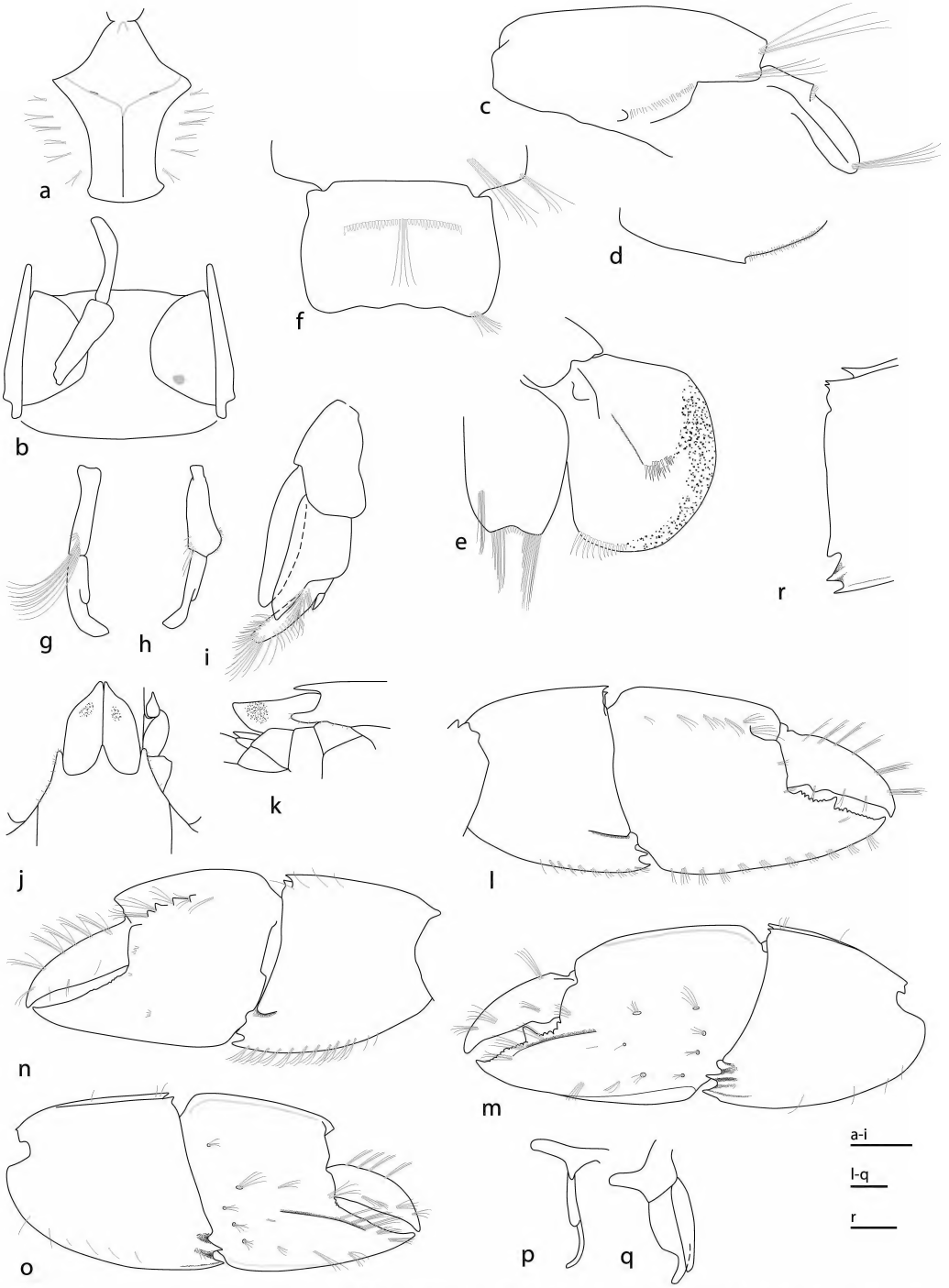

Figure 21. *Eucalliaxiopsis paradoxa* sp. nov. Holotype, NMV J71683 (male, 9.4 mm): a, thoracic sternite 7; b, pleonite1 sternite, right pleopod 1 (anterior uppermost); c, pleonite 6, telson, lateral view; d, pleonite 6, left lateral oblique view; e, right uropod; f, telson; g, h, pleopod 1, mesial and posterior views; i, pleopod 2, posterior view. Paratype, NMV J71679 (ovigerous female, 9.4 mm): j, k, anterior carapace, eyestalks, antenna, dorsal and lateral views; l, m, major cheliped (left), mesial and lateral views; n, o, minor cheliped (right), mesial and lateral views; p, q, pleopods 1, 2. Paratype, NMV J71684 (female, 10.4 mm): r, minor cheliped carpus, distolateral margin. Scale bars = 1 mm.

rostrum, with rounded apex, anteriorly directed, with numerous submarginal dorsal setae.

Thoracic sternite 7 1.3 times as long as wide, with well-defined median sulcus over posterior half, lateral groove anterior to coxal articulation shallow, oblique, meeting medially, with 7 posterolateral clusters of 2 or 3 long setae. Pleonal sternite 1with pair of swollen relatively unchitinised areas anterior to ridge bearing pleopods. Pleonite 6 with small lateral blunt hook-like process at midpoint.

Eyestalk 2.2 times as long as wide at base, tapering to cornea and acute apical lobe; cornea subcircular; apical lobe extended dorsally. Antennular peduncle 3 times as long as width of both eyestalks; article 2 3.5 times as long as wide; article 3 half as long as article 2; articles 2 and 3 with ventrolateral row of long setae, continued onto flagellum. Antennal peduncle 3.4 times as long as width of both eyestalks, overreaching antennule peduncle by half of article 5; scaphocerite wider than long, with acute apex; article 4 c. 5 times as long as wide; article 5 0.6 length of article 4. Maxilliped 3 ischium with slightly convex mesial margin, expanding from narrow proximomesial corner; ischium–merus upper margin 1.7 times as long as greatest width; crista dentata of 12 spines, the most proximal reflexed; carpus–dactylus together almost as long as ischium–merus.

Chelipeds unequal, major propodus 1.2 times as long as that of minor, both of similar widths, major dactylus stouter than that of minor. Major cheliped (right in holotype) ischium twice as long as distal width, lower margin with short spines becoming more distinct distally; merus twice as long as broad, lower margin mostly straight, unarmed, upper margin with distal tooth; carpus 1.2 times as wide as upper length, upper margin carinate, unarmed except for distal tooth, distomesial margin with prominent lobe near lower margin, distolateral margin with acute tooth near upper margin, with 3 acute teeth near lower margin separated by submarginal oblique grooves, second tooth with prominent rounded ridge, 3 short setae in lower groove; propodus widest proximally, tapering, upper palm length barely exceeding greatest width, upper margin straight, carinate, with rounded lobe not projecting over dactylus, lower margin carinate, strongly curved mesially, mesial face with short distal uneven setose ridge below upper margin, distomesial margin of palm almost straight, lateral face of palm with short horizontal ridge, about fifth length of palm, extending on to finger, 4 rimmed tubercles near proximal margin, 1 at midpoint of palm, 1 near lower margin, each perforated for cluster of setae; fixed finger half length of upper margin of palm, cutting edge with denticles over proximal half, blunt triangular tooth near midpoint; dactylus as long as fixed finger, twice as long as wide at base, cutting edge with blunt proximal molar, with straight tip; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers.

Minor cheliped (left in holotype) ischium twice as long as distal width, lower margin with distal spines; merus twice as long as broad, lower margin mostly straight, unarmed; carpus 1.2 times as wide as upper length, upper margin carinate, unarmed except for distal tooth, distomesial face with lower submarginal ridge, distolateral margin with acute tooth near upper margin, with 3 teeth near lower margin separated by submarginal oblique grooves, second tooth acute with prominent rounded ridge, 2 short setae in lower groove; propodus greatest width proximally, tapering, upper palm length equal to greatest width, palm tapering, upper margin carinate, overhanging mesial face, with rounded lobe projecting over dactylus, lower margin carinate, strongly curved mesially, mesial face with 4 blunt teeth at associated with upper row of clusters of setae, distomesial margin of palm almost straight, lateral face of palm with prominent ridge running from two-thirds length of palm to middle of finger, 5 rimmed tubercles near proximal margin of which 1 near midpoint of palm is more distal, each perforated for cluster of setae; fixed finger 0.7 length of upper margin of palm, width at base half width of palm, cutting edge smooth; dactylus as long as fixed finger, 3.2 times as long as wide at base, cutting edge straight; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers.

Pereopod 2 merus twice as long as maximum width; dactylus c. 3 times as long as upper margin of propodus. Pereopod 3 merus twice as long as maximum width; carpus 1.8 times as long as wide; propodus with lower margin concave, twice as long overall as mid-length; dactylus 0.7 times length of axial length of propodus. Pereopod 4 merus length 2.2 times maximum width; carpus 2.5 times as long as wide; propodus as long as wide, typically setose, with 1 long distal seta overlapping dactylus.

Pleopod 1 article 1 distally setose; article 2 as long as article 1, 4 times as long as wide, with apex curved, appendix interna lobe-like, not produced, unarmed. Pleopod 2 endopod twice as long as wide; appendix masculina overreaching endopod by about third its length, triangular in cross-section, setose along posterior face and distally; appendix interna near base of appendix masculina without hooks.

Uropodal endopod anterior margin convex, posterior margin convex, widest about third way along, 1.4 times as long as wide, apex excavate, with rows of long setae at ends of anterior and posterior margins, with 8 short setae between in excavation, with subdistal group of facial setae; exopod ovate, anterior margin straight, distal and posterior margins continuous, greatest dimension 2.2 times anterior margin, with row of blade-like distal setae on distal margin, c. 6 not overlapping with densely setose distal margin; dorsal plate extending almost half of exopod width, distal margin with spiniform setae. Telson 1.6 times as wide as long, broadest at midpoint, posterolateral corner rounded; posterior margin sinuous, lateral regions most prominent, with posterolateral cluster of long setae plus 2 short spiniform setae; dorsal surface with sharp transverse ridge at anterior third, with 36 short spiniform setae, few long setae at midpoint

Female. Essentially as male except: major cheliped palm tapering, upper length 0.9 greatest width, upper margin convex, depressed distally, lateral ridge longer than in male, fixed finger broader than in male, crenellate proximal and distal to tooth. Pleonal sternite 1with pair of oval plates supporting pleopods, each with longitudinal row of setae. Pleopod 1 peduncle with

mesial setose lobe longer than base. Pleopod 2 peduncle with similar mesial setose lobe; endopod without appendix interna.

Etymology. Paradoxa (Latin), reflecting the subtle differences from *E. panglaoensis* and co-occurring *E. dworschaki*, and a tribute to the collector's name, Martin Riddle.

Distribution. Australia, Qld, central Great Barrier Reef (18° S). Subtidal coral reef lagoons.

Remarks. Eucalliaxiopsis paradoxa shares several features with *E. panglaoensis* and *E. dworschaki* (see remarks under *Eucalliaxiopsis* above).The new species differs from these two in having eight short setae in the uropodal endopod excavation (fig. 21e; 11 in the other species), a short longitudinal ridge at the base of the finger on the lateral face of the chelipeds, the propodus of the male cheliped tapering (more rectangular in the others), and the middle distolateral cheliped carpal tooth being oblique and sharply ridged (figs 20g, i, 21m, o, r, 25h). In *E. dworschaki*, the ridge on the palm extends almost its entire length, and the middle carpal lobe is perpendicular and with a median groove. Besides having fewer short setae at the end of the uropodal endopod, *Eucalliaxiopsis paradoxa* differs from *E. panglaoensis* in the upper margin of the male major cheliped palm being as long as wide (vs 1.3 times as long as palm width), the palm of the female major cheliped being relatively longer (1.1 vs 0.9 times as long as greatest width), the uropodal endopod being more tapered (more oval in *E. panglaoensis*) and the sinuous posterior margin of the telson (vs straight).

Eucalliaxiopsis patio sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:F5884500-4430-493B-9BCD-CA5E769F846E

Figures 22–24

Eucalliaxiopsis PNG-1153C.— Robles et al., 2020.

Material examined. Holotype. Papua New Guinea, New Ireland Province, Patio Island, 02° 36.2' S, 150° 31.6' E, 6–8 m, coral rubble (KAVIENG 2014 stn KB38), MNHN-IU-2014-2536* (female, cl. 4.6 mm).

Paratype. Collected with holotype (MNHN-IU-2014-2539 (male, cl. 4.3 mm, with male and female bopyrid isopods under left branchiostegite).

Diagnosis. Pleonite 1 without pair of sternal plates. Eyestalk 1.5 times as long as wide. Antennule peduncle reaching to midpoint of antenna peduncle article 5. Maxilliped 3 exopod absent. Cheliped carpi distolateral margin square at lower angle, propodi lateral face without longitudinal ridge, upper mesial face with row of short transverse ridges associated with more distal clusters of setae. Male pleopod 1 of single article with narrower distal lobe. Female pleopod 2, appendix interna present. Uropod endopod ovate. Telson without transverse row of spiniform setae.

Description of holotype female. Carapace length 4.6 mm, smooth; gastric–abdominal regions together 4.2 times as long as wide; branchiostegite fully calcified; cervical groove at 0.67 carapace length, scarcely obvious on branchiostegite; cardiac sulcus at 0.83 carapace length, not meeting mid-dorsally, extending transversely across two-thirds of branchiostegite.

Rostrum broadly rounded-triangular, length about 0.2 width of eyestalks. Anterolateral carapace lobe as long as rostrum, with rounded apex, depressed anteriorly, with c. 5 submarginal dorsal setae. Pleonites 1–6 lengths relative to cl: 0.46 : 0.67 : 0.45 : 0.33 : 0.41: 0.51; pleonite 1 with strong dorsal transverse groove, without pair of sternal plates; pleonites 3–5 with lateral tufts of setae; pleonite 6 with 8 lateral rows of setae.

Thoracic sternite 7 1.2 times as long as wide, with well-defined median sulcus over posterior half, smooth over medial half, lateral ridge anterior to coxal articulation crossing pit at quarter of width, meeting medially, with 3 posterolateral clusters of long setae.

Eyestalk 1.7 times as long as wide at base, swollen laterally, tapering to cornea and acute apical tubercle; cornea wider than long, depressed anteriorly. Antennular peduncle twice as long as width of both eyestalks; article 2 twice as long as wide; article 3 as long as article 2; articles 2 and 3 with ventrolateral row of long setae, continued onto flagellum. Antennal peduncle 2.4 times as long as width of both eyestalks, overreaching antennule peduncle by half of article 5; scaphocerite ovoid, longer than wide; article 4 c. 5 times as long as wide; article 5 0.8 length of article 4. Maxilliped 3 ischium with slightly convex mesial margin, expanding from narrow proximomesial corner; ischium–merus upper margin twice as long as greatest width; crista dentata of 6 spines, the 2 most proximal largest; carpus–dactylus together almost as long as ischium–merus.

Chelipeds unequal, major carpus-propodus upper margin 1.1 length of minor, propodus 1.2 times as wide as minor. Major cheliped (left in holotype) ischium twice as long as distal width, lower margin with needle-like spines becoming more distinct distally; merus 1.7 times as long as broad, lower margin convex, unarmed; carpus 1.2 times as wide as upper length, margins carinate; propodus greatest width in middle of palm, upper palm length 1.15 times greatest width, distomesial margin of palm with submarginal group of 2 setae, small tubercle, distolateral margin of palm with submarginal group of c. 6 setae between fingers; fixed finger 0.4 length of upper margin of palm, cutting edge with microdenticles over proximal half, blunt triangular tooth at about midpoint; dactylus as long as fixed finger, twice as long as wide at base, cutting edge with deflected tip; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers; 3 short transverse ridges associated with setae on submesial upper margin.

Minor cheliped (right in holotype) ischium c. 2.3 times as long as distal width, lower margin with needle-like spines becoming more distinct distally; merus 1.7 times as long as broad, lower margin convex, unarmed; carpus 1.2 times as wide as upper length, margins carinate; propodus palm more tapering than major, 0.95 times as wide as upper palm length, distomesial margin of palm with submarginal group of 4 12 setae, distolateral margin of palm with submarginal group of c. 4 setae; fixed finger half length of upper margin of palm, mesial cutting edge straight, smooth, cutting edge straight, fixed finger with smooth lateral ridge defining edge of lateral concavity at base of fixed finger, without granules; dactylus as long as fixed finger, 3 times as long as wide at base, cutting edge straight; submarginal tufts of long setae on upper and lower mesial

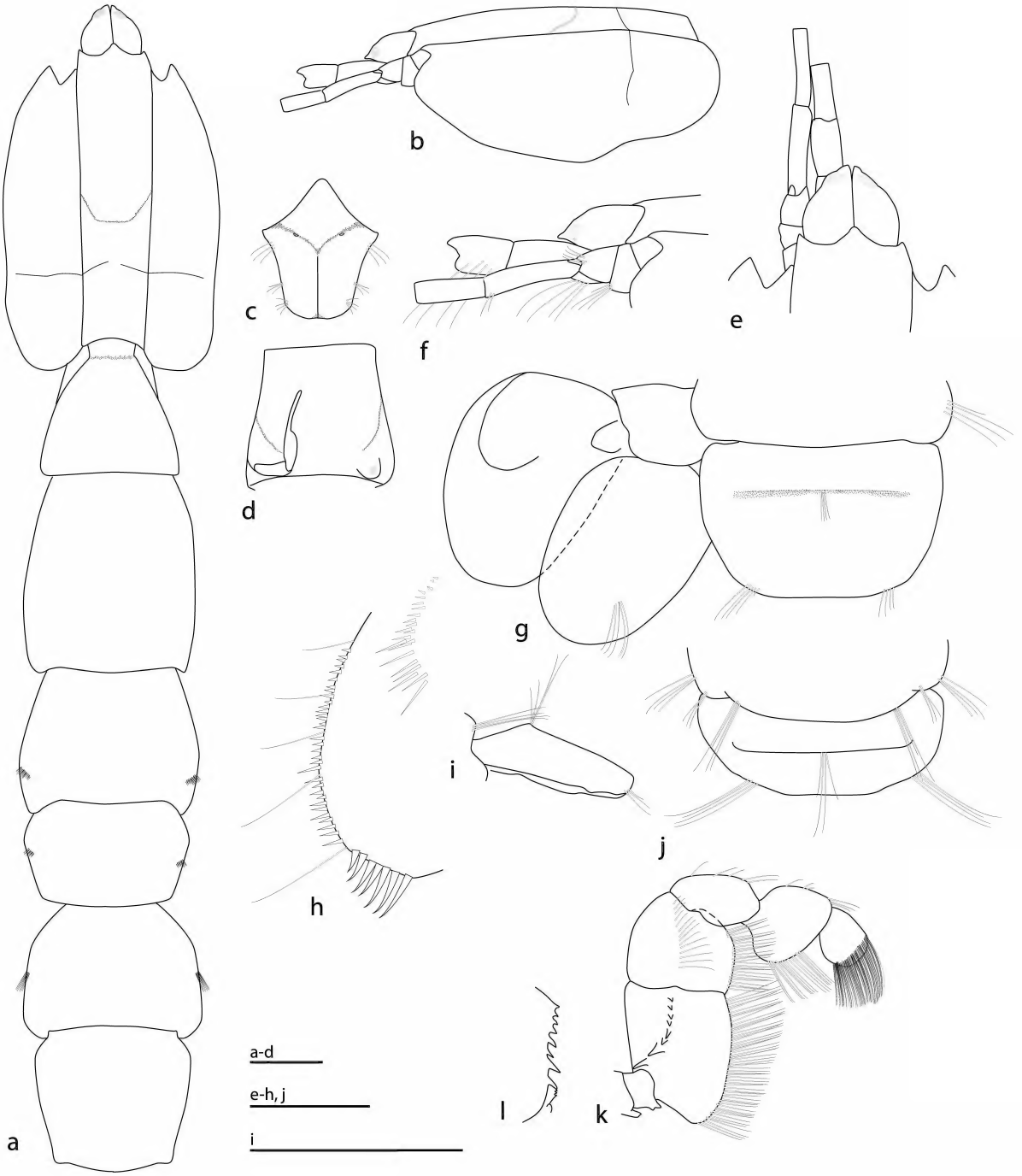

Figure 22. *Eucalliaxiopsis patio* sp. nov. Holotype, MNHN-IU-2013-2536 (female, 4.1 mm): a, habitus, dorsal; b, carapace, lateral view; c, thoracic sternite 7; d, pleonite1 sternite, right pleopod 1; e, f, anterior carapace, eyestalks, antennule, antenna, dorsal and lateral views; g, pleonite 6, telson, uropod; h, uropod exopod, margin, dorsal plate; i, j, telson, lateral and dorso-anterior views; k, maxilliped 3; l , maxilliped 3, crista dentata, basis, ischium. Scale bars = 1 mm.

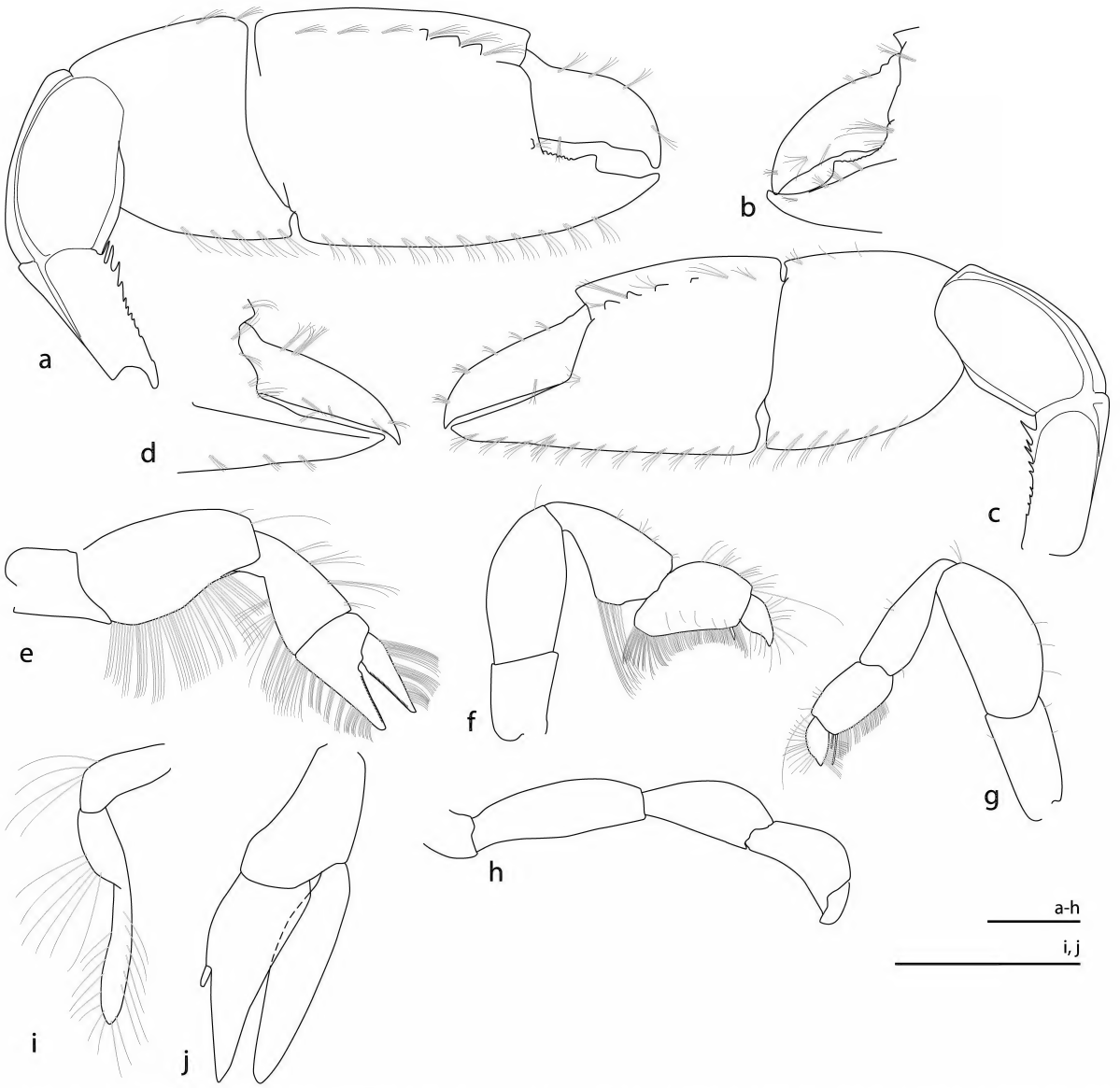

Figure 23. *Eucalliaxiopsis patio* sp. nov. Holotype, MNHN-IU-2013-2536 (female, 4.1 mm): a, major cheliped (left), mesial; b, major cheliped (left), distal propodus, dactylus, lateral; c, minor cheliped (right), mesial view; d, minor cheliped (right), distal propodus, dactylus, lateral; e–h, pereopods 2–5; i, j, pleopods 1, 2. Scale bars = 1 mm.

margins of carpus and propodus, opposing mesial margins of fingers; 2 short transverse ridges associated with setae on submesial upper margin, more prominent distally.

Pereopod 2 merus 1.8 times as long as maximum width; dactylus c. 3 times as long as upper margin of propodus. Pereopod 3 merus 2.2 times as long as maximum width; carpus 1.8 times as long as wide; propodus with lower margin almost straight, 1.8 times as long as mid-length; dactylus half as long as axial length of propodus. Pereopod 4 merus twice as long as maximum width; carpus 3 times as long as wide; propodus typically setose, with distal spiniform setae among setose margin, with 2 long distal setae overlapping dactylus.

Pleopod 1 article 1 without distal projection beyond article 2; article 2 longer than article 1. Pleopod 2 endopod 3 times as long as wide; appendix interna at midpoint of endopod.

Uropodal endopod ovoid, anterior margin more convex

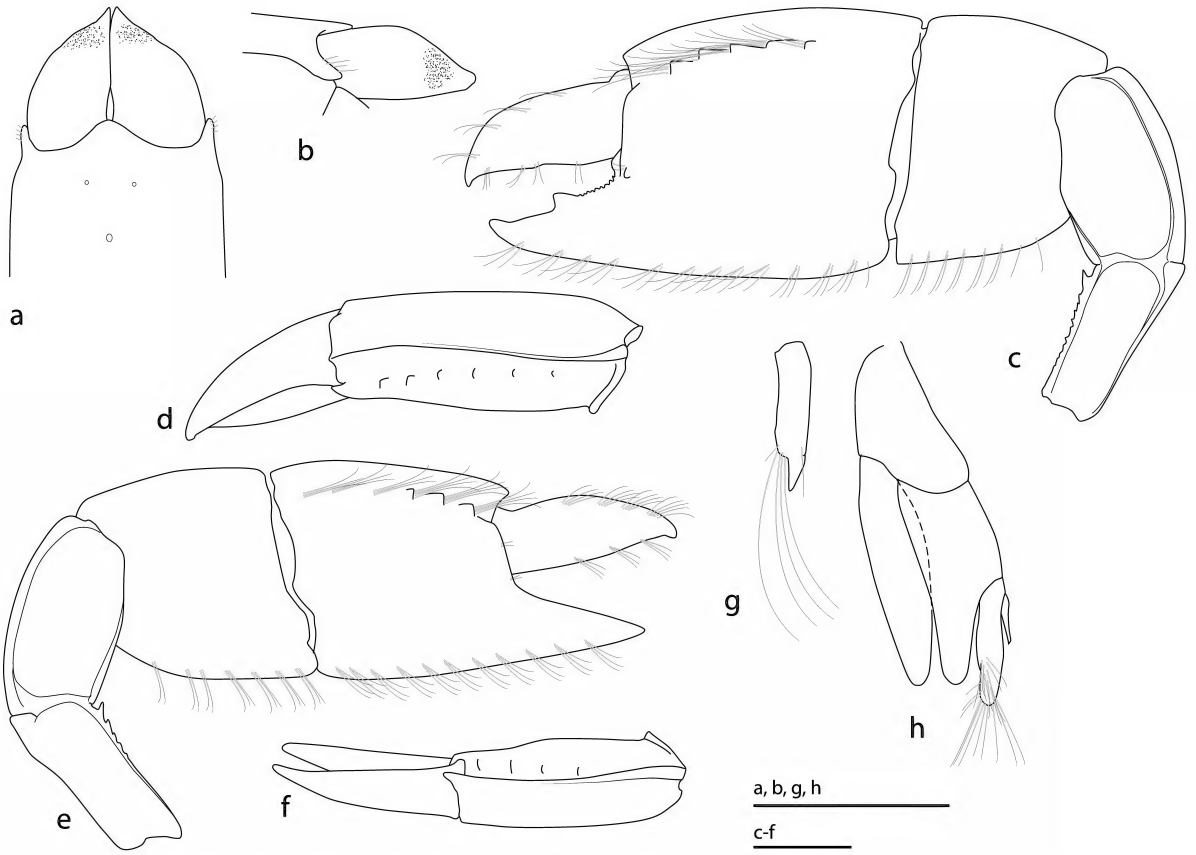

Figure 24. *Eucalliaxiopsis patio* sp. nov. Paratype, MNHN-IU-2013-2539 (male, 4.6 mm): a, b, anterior carapace, eyestalks, dorsal and lateral views; c, major cheliped (right), mesial; d, major cheliped (right), propodus, dactylus, upper; e, minor cheliped (left), mesial view; f, minor cheliped (left), propodus, dactylus, upper; g, h, pleopods 1, 2. Scale bars = 1 mm.

than posterior margin, widest about third way along, 1.5 times as long as wide, with subdistal group of facial setae; exopod ovate, anterior margin straight, distal and posterior margins continuous, greatest dimension 2.2 times anterior margin, with row of blade-like distal setae on distal margin, c. 6 not overlapping with densely setose distal margin; dorsal plate extending almost half of exopod width, distal margin with spiniform setae. Telson 1.6 times as wide as long, broadest over anterior half, posterolateral corner evenly rounded to posterior margin; posterior margin barely convex, with posterolateral clusters of long setae; dorsal surface with obscure rounded transverse ridge at anterior third, without median notch.

Paratype male. Carapace length 4.3 mm. Eyestalks 1.5 times as long as wide at base, swollen laterally, tapering to cornea and acute apical tubercle; cornea wider than long, depressed anteriorly Postrostral dorsal area with pair of shallow pits.

Chelipeds unequal, major carpus-propodus upper margin 1.1 length of minor, propodus 1.3 times as wide as minor. Major cheliped (right) ischium twice as long as distal width, lower margin with denticles, 1 distal spine; merus 1.7 times as long as broad, lower margin convex, unarmed; carpus 1.4 times as wide as upper length, margins carinate; propodus greatest width in middle of palm, upper palm length 1.15 times greatest width, distomesial margin of palm with submarginal group of 2 setae plus tubercle; fixed finger 0.35 length of upper margin of palm, cutting edge with microdenticles over proximal half, blunt triangular tooth near midpoint; dactylus as long as fixed finger, twice as long as wide at base, cutting edge irregular, with deflected tip; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers; 4 short transverse ridges associated with setae on submesial upper margin.

Minor cheliped (left) ischium c. 2.3 times as long as distal width, lower margin with denticles, 1 distal spine; merus 1.8 times as long as broad, lower margin convex, unarmed; carpus 1.1 times as wide as upper length, margins carinate; propodus palm more tapering than major, 0.95 times as wide as upper palm length, distomesial margin of palm with 2 submarginal

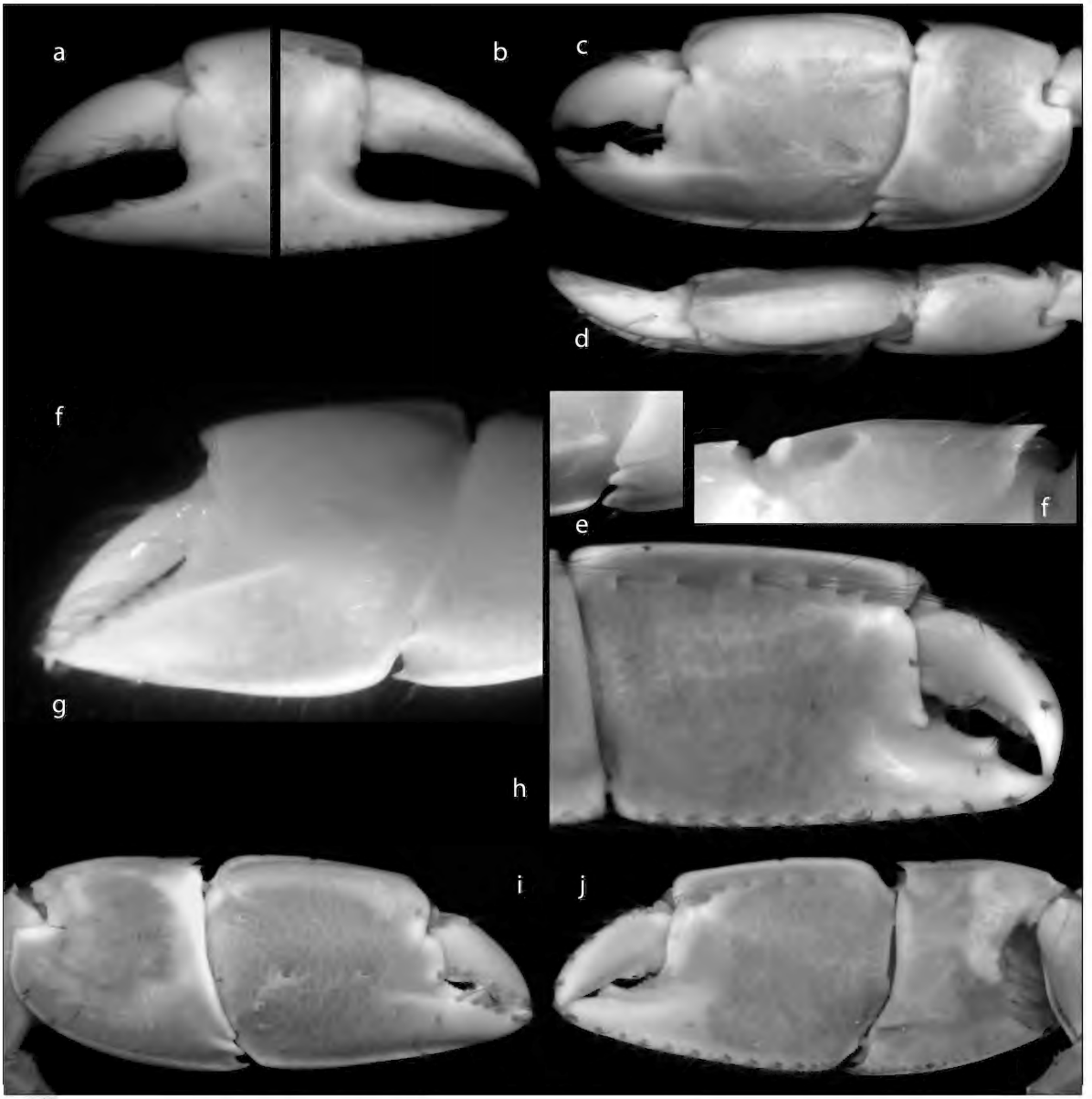

Figure 25. *Eucalliaxiopsis* spp. *E. aequimana*: a, b, major cheliped, mesial. *E. dworschaki*, Papua New Guinea, MNHN-IU-2013-10003: c, d, major cheliped lateral, upper margin. *E. dworschaki*, Philippines, NHMW 20923: e, f, major cheliped carpus lower lateral angle, upper margin. *E. panglaoensis*, NHMW 20922: g, minor cheliped, lateral. *E. inaequimana*: h, major cheliped, mesial. *E. paradoxa*: h, i, major cheliped lateral, mesial. Photos e–g: P.C. Dworschak. Various scales.

groups of 2–3 setae; fixed finger 0.4 length of upper margin of palm, mesial cutting edge straight, smooth; dactylus as long as fixed finger, 2.8 times as long as wide at base, cutting edge straight; submarginal tufts of long setae on upper and lower mesial margins of carpus and propodus, opposing mesial margins of fingers; 3 short transverse ridges associated with setae on submesial upper margin, more prominent distally.

Pleopod 1 articles indistinguishable; article 1 with 1 short, 4 long distal setae; article 2 a short triangle, half as wide as article 1. Pleopod 2 endopod 2.7 times as long as wide; appendix masculina attached at mid-length, 5 times as long as width, distal margin rounded, exceeding endopod by fifth of its length, with c. 9 facial setae near midpoint, c. 14 subdistal setae; appendix interna rod-like, about 0.4 length of appendix interna.

Etymology. From Patio Island, Papua New Guinea, the type locality (noun in apposition).

Distribution. Papua New Guinea. Coral rubble, 6–8 m.

Remarks. The holotype was sister taxon to five individuals of *E. inaequimana* on the phylogenetic tree of Robles et al. (2020). Both species have submarginal mesial transverse ridges on the cheliped propodi from which tufts of long setae emerge; in other species of *Eucalliaxiopsis* the same tufts are not supported in this way. The male pleopod 1 of both species has a simple second article, free or fused, a form seen too in *E. madagassa* (see Poore and Dworschak, 2017: fig. 1C, D), *Eucalliax quadracuta* and *Calliaxina bulimba* (see above). The typical article 2 of species of *Eucalliaxiopsis* is flattened with a distal oblique notch. *Eucalliaxiopsis patio* differs from *E. inaequimana* in shorter, more swollen eyestalks (1.5 vs 1.8 times as long as wide), slightly shorter rostrum (quarter vs fifth length of eyestalk), shorter antenna peduncle (2.4 vs 3.0 times as long as base of both eyes), more compact antennular and antennal peduncular articles, the telsonic ridge being only slightly elevated and complete (vs clearly elevated, with median notch), and a broader uropodal endopod (1.5 vs 1.8 times as long as wide). The appendix interna on the female pleopod 2 is present while it is absent in *E. inaequimana*. It is possible that this difference may be related to the female's small size; Dworschak (2006) noted that the smallest female of *E. panglaoensis* possessed an appendix interna while larger ones did not. Two individuals were collected from the type locality, with carapace lengths of 4.3 and 4.6 mm. The largest known specimen of *E. inaequimana* has a carapace length of 9.1 mm.

Identification of these specimens using Sakai's (2011) key to species of *Calliaxina* leads to *C. aequimana*, a southern Australian species. This species, now *Eucalliaxiopsis aequimana*, lacks mesial ridges on the chelipeds and has a female-like male pleopod 1.

Pseudocalliax Sakai, 2011

Pseudocalliax Sakai, 2011: 505–506.—Sakai, 2018: 744.—Poore et al., 2019: 128, 146, figs 18a, k, 19e, r.

Remarks. The type and only species was placed in Eucalliacinae, now Eucalliacidae, as a species of *Calliax*, by Sakai (2005). Sakai (2011) erected the new genus *Pseudocalliax* for it in the same subfamily. No molecular sequences were available to Robles et al. (2020) to challenge this placement that has good morphological support (Poore et al., 2019). The genus shares with the three species of *Calliax* the characteristic short fixed finger on the minor cheliped.

Pseudocalliax tooradin (Poore and Griffin, 1979)

Figure 26

Callianassa tooradin Poore and Griffin, 1979: 275–277, fig. 36.

Calliax tooradin.—Sakai, 1988: 61.—Davie, 2002: 459.—Sakai, 2005: 204.

Paraglypturus tooradin.—Sakai, 1999: 124, fig. 33a–c.—Poore, 2004: 184, fig. 50h, i.

Pseudocalliax tooradin.—Sakai, 2011: 506.

Material examined. Australia, Vic., Western Port, Crib Point, 38° 20.23' S, 145° 13.38' E, 5 m (CPBS stn 11N), NMV J301 (holotype female, 5.2 mm), NMV J302 (2 paratype females); 38° 21.17' S, 145° 13.15' E, 2 m (CPBS stn 000), NMV J303 (paratype male, 6.5 mm). San Remo, channel edge, E. of No. 7 beacon, 38° 32' S, 145° 23' E (MRG Transect 1), NMV J59760 (male, 5.1 mm); N from 200 m E of Back Beach Rd to channel edge, 38° 32' S, 145° 23' E (MRG transect 2), NMV J59761 (2 males, 4.2, 6.0 mm). Swan Bay, Edwards Point, 38° 13.3' S, 144° 41.4' E, 2 m, NMV J16722 (juvenile, 1.5 mm).

Distribution. Australia, Vic., entrances of Western Port and Port Phillip Bay. Subtidal, c. 2 m.

Remarks. Poore and Griffin (1979) provided only a short description and simple figures. Here, the antennae, chelipeds, terminal articles of pereopods 3 and 4, male pleopods, telson and uropod are figured. The species is notable for the setose thoracic sternite 7 and ventroposterior surface of the coxa–ischium of pereopod 5, a feature diagnostic for the genus (fig. 26b). The antenna bears a free scaphocerite, longer than broad, with a rounded apex (fig. 26a). The exopod of maxilliped 3 typically reaches the middle of the merus but is shorter on smaller individuals. While the fixed finger of the minor cheliped is shorter than the dactylus in most individuals it is almost as long in one male. The propodus of pereopod 3 is suboval, little longer along its upper margin than its greatest width, and densely setose on its lateral face. The propodus of pereopod 4 is elongate-oval, 1.5 times as long along its upper margin than its greatest width, with a distal long spiniform setae on the lower margin, and densely setose on its lateral face. The male pleopod 1, overlooked by Poore and Griffin (1979), has a shorter second article with an apical notch (fig. 26g). The peduncle of the male pleopod 2 is longer than broad; the appendix interna is short and lacks hooks; no appendix masculina is present (fig. 26h). The appendix interna on the endopod of pleopod 3 is triangular, longer than broad, emerging by about half its length (fig. 26j). The uropodal endopod is oval, 1.8 times as long as wide, with marginal setae; the exopod is 1.6 times as long as wide, with short spiniform setae along its apical margin, with a well-defined dorsal plate with c. 6 short spiniform setae and many longer setae (fig. 26f). A dorsal oval, cardiac prominence and cardiac sulcus are all absent; all known material is in NMV (cf. contradictory statements and figures in Sakai, 1999, and Sakai, 2011).

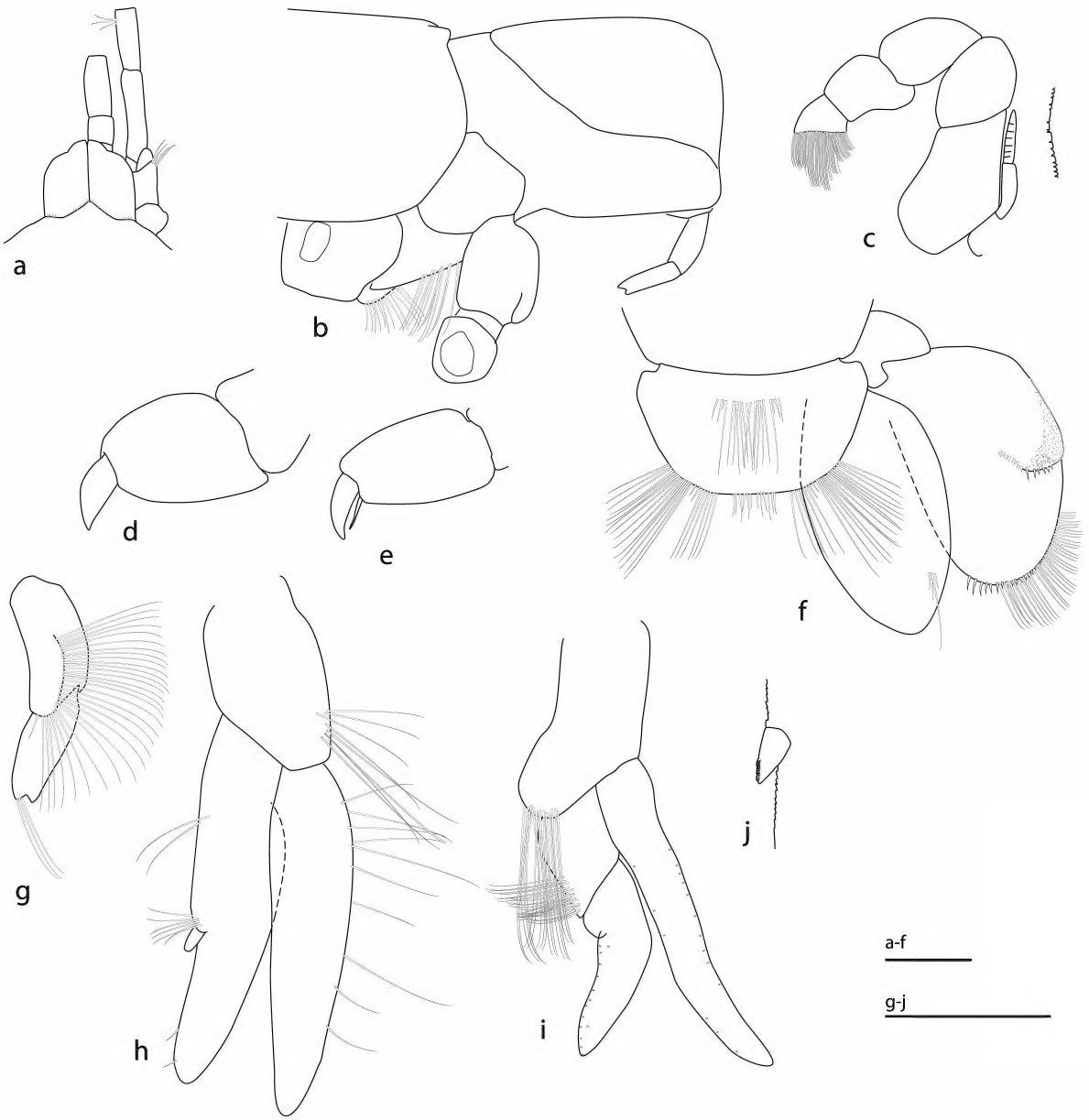

Figure 26. *Pseudocalliax tooradin* Poore and Griffin, 1979. Australia, Vic., Western Port, NMV J303 (paratype male, 6.5 mm): a, anterior carapace, eyestalks, antennule, antenna; b, posterior carapace, pleonite 1, coxa 4, thoracic sternite 7, coxa-basis 5, pleopod 1; c, maxilliped 3, with crista dentata; d, e, propodus, dactylus, pereopods 3, 4; f, telson, uropod; g, pleopod 1; h, pleopod 2; j, appendix interna, pleopod 3. NMV J301 (holotype female, 5.2 mm): i, pleopod 2. Scale bars = 1 mm.

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Initiation and early development of the postcanine deciduous dentition in the dasyurid marsupial *Dasyurus viverrinus*

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Abstract

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There has been disagreement for more than 100 years concerning the presence or absence of deciduous and successional third premolars in the dentition of the Australian dasyurid marsupial *Dasyurus viverrinus* as well as in other species of the genus *Dasyurus*. Most authors during the 19th and 20th centuries have considered the missing premolar in *Dasyurus* to be the third premolar family in both jaws, in part because of the reduction in size of the third deciduous premolar in many other genera of dasyurids. While other authors, found "the deciduous premolar to be constantly present in the young mammary foetus as a small and precociously calcified vestigial tooth". However, the fate of this deciduous tooth, and its possible successor in later developmental stages, was never described; and the vestigial dp3 and its possible successor were assumed to undergo absorption during foetal life. With access to later developmental stages of *Dasyurus viverrinus*, via the extensive collections of Professor J.P. Hill, we present new evidence for the later development of dP3 and P3 in both jaws, the probable eruption of the successional P3 in both jaws and evidence that dP2 is the missing tooth in both jaws of this dasyurid species.

Keywords

Dasyurus, deciduous dentition, dental development, dental homologies, pouch young

Introduction

During the years 1895–1905, when he was a Demonstrator of Biology at the University of Sydney, Australia, Professor James P. Hill collected a large sample of juveniles of the dasyurid marsupial *Dasyurus viverrinus*, ranging from newborn young to individuals about four months old. The species was still relatively common in New South Wales at the time and the animals lived relatively well in captivity. Many of these captive-bred dasyurids produced the dated pouch young that are the subject of this paper. Although Hill and colleagues published several papers on the early development, placentation and reproduction in general of *Dasyurus*, only one paper dealt specifically with the development of the pouch young.

An extensive series on the development of the growth stages in the pouch young of *Dasyurus viverrinus* was examined in a monograph by Hill and Osman Hill (1955). The authors presented 16 figures of the pouch young, and they described in detail the external morphology of the developing young in a series of stages labelled A to P. These ranged from unattached newborn young outside and inside the pouch, measuring 5.5–6.0 mm greatest length (GL) and 2.5 mm head length (HL; stage A), up to adolescent young that were four months old (stage P). These oldest young were freely moving about outside the pouch and measured about 60 mm HL. However, no description or figures of the microscopic anatomy of the developing teeth were presented. Unfortunately, Hill passed away in 1954 during the preparation of their manuscript. We suspect that Hill would have published a detailed description of the developing dentition if he had lived longer. After his death, at least a portion of his collections of mammalian embryos and young animals was donated to the Hubrecht Laboratory of Comparative Embryology, Utrecht, Netherlands. These included a series of histological sections of some of the *Dasyurus viverrinus* pouch young described by Hill and Osman Hill (1955) and some older juveniles preserved as alcohol specimens. A few of the alcohol specimens from Hill's collection were borrowed and sectioned by Professor Louis Bolk, University of Amsterdam, Netherlands, and then returned to the Hubrecht Laboratory of Comparative Embryology.

Materials and methods

It is rare to be able to histologically examine closely related stages of early developing pouch young for any marsupial, and we were able to study three unattached intrauterine embryos and 22 early developing stages of pouch young attached to the nipple for *Dasyurus viverrinus* from the Hill collection. The pouch young examined range in age from about 30 hours old, measuring about 6 mm GL, to 40–41 days old, and measuring about 29 mm GL. Given that this species appears to be a useful model for the developmental relationships of the dentition in the extinct dasyuromorphian *Thylacinus cynocephalus* (see Luckett et al., 2019), along with other marsupicarnivore taxa, we present this overview of early dental development in *Dasyurus viverrinus*. These studies were carried out over a period of several years at the Hubrecht Laboratory of Comparative Embryology before the embryological collections were transferred to their present home in the Museum für Naturkunde, Berlin, Germany.

It should be noted that *Dasyurus viverrinus* is probably extinct on mainland Australia, with a last sighting on January 1963 in the suburbs of Sydney (Dickman et al., 2001). The species persists in Tasmania , although it is vulnerable there for several reasons, including climate change and disease, among other possibilities (Fancourt, 2016).

A brief overview of our findings on dental development in *Dasyurus* was presented previously (Luckett, 1989, 1993). We have made new drawings of four of the developing pouch young (fig. 1) examined by us from the Hill collection, ranging from an early attaching pouch young of about 30 hours old to an embryo of about 41 days old, measuring about 29 mm GL and 18 mm HL. Most genera of dasyurids, peramelids and didelphids have three premolars in both jaws of adults. This is presumably the primitive condition for marsupials (Cifelli et al., 1996). Emphasis in our study is given to the evidence for loss of dP2 in this dasyurid with two premolars, and the accelerated development of dP3 and P3, when compared with these features in dasyurids with three premolars. A summary of the major features of early development for the deciduous and successional dentition in marsupials is presented in fig. 2.

Results

Early development of the dental lamina

Hill and Osman Hill (1955) noted that the earliest date of gestation was 16 days in their sample of *Dasyurus viverrinus* embryos. The earliest evidence of a dental lamina that we found was detected in the maxilla of three intrauterine embryonic stages of 5.5–6 mm GL. In the youngest of these embryos, the dental lamina was detected bilaterally in the upper jaw as a localised thickening of the oral epithelium that was associated with a very early differentiation of bone (or prebone) in the distal portion of the developing maxilla. In contrast, the dental lamina and developing bone were not yet detected in the premaxillary region of the upper jaw. The more mature intrauterine young showed dental lamina thickenings in both the premaxilla and maxilla regions of the upper jaw. The dental lamina was not yet evident in the lower jaw of the youngest intrauterine embryo. As explained by Hill and Osman Hill (1955), the newborn young of *Dasyurus viverrinus* are able to find their way to the mother's pouch, unaided by the mother and helped by their own well-developed forelimbs that have very sharp deciduous claws.

In the youngest pouch young attached to the mother's nipple, examined at about 30 hours old and measuring 6 mm GL, a continuous dental lamina was present bilaterally in both the upper and lower jaws. This specimen was illustrated as fig. 5 by Hill and Osman Hill (1955) and we have redrawn this important specimen in our fig. 1a. The HL of this pouch young was 3.25 mm. It should be noted here that all of our measurements from the Hill collection are taken from specimens that had been placed in spirit fixation by Hill. In the upper jaw, three early-bud thickenings are evident on the dental lamina (see fig. 2a for the relations between the dental lamina and an early bud). The most rostral of these is associated with the premaxillary ossification, the next is adjacent to the rostral end of the developing maxillary bone, and the distal bud occurs at the caudal end of the dental lamina and is associated with the distal extent of the maxillary ossification. Based on their bony relationships and comparison with later ontogenetic stages, these tooth buds can be identified as dI2 or dI3 anteriorly, dC and dP3, respectively. The dP3 bud lies beneath the level of the anterior half of the eye. An overview of the major features of dental development for the postcanine dentition in the upper and lower jaws is summarised in Tables 1 and 2.

The bud for the early developing incisors in the upper jaw does not occur at the rostral-most extent of the premaxilla; instead, it is positioned somewhat more distolateral. It is unclear whether this developing tooth germ is dI2 or dI3 at this early stage. The late or retarded development of dI1 in the upper jaw of dasyurids, peramelids and didelphids was noted by Thomas (1887). Later, Guiler and Heddle (1973) suggested that the late development and eruption of dI1 helped the continued suckling of the young. In the lower jaw, a large early bud is evident at the rostral extent of the dentary ossification. Two small bud-like thickenings occur distal to the rostral early bud (presumably di1), but these are not as distinct as the di1. It should be noted here that adult dasyurids possess four upper and three lower incisors, in contrast to the presumably primitive condition in ancestral marsupials and didelphids, which possessed five upper and four lower incisors. It is unclear to us which incisor has been lost in each jaw of *Dasyurus*, so we will simply call them I1-4 above and i1-3 below.

We next examined a three-day-old embryo measuring 7 mm GL and 4 mm HL (see fig. 6 in Hill and Osman Hill, 1955). Two small deciduous incisors were in an early-bud stage rostrally in the upper jaw. The moderately sized deciduous canine was in a more distinct early-bud stage. It had a more darkly stained abnormal buccal portion and a more normal pale-stained lingual portion. Based on later developing stages, the darkly stained buccal portion represents the primordium of the rudimentary deciduous canine, and the more normal lingual portion represents the primordium of the successor canine. These modified relationships for the developing deciduous and successional incisors and canines were

Table 1. Development of *Dasyurus viverrinus* upper postcanine dentition

Stage	dP1	dP2	dP3	P3	M1	M2	M3	M4
30 hour PY 6 mm GL (3.25 mm HL)	No trace	No trace	Early bud					
3 day PY 7 mm GL (4 mm HL)	No trace	No trace	Early to middle bud					
5–6 day PY 8 mm GL (4.5 mm HL)	No trace	No trace	Early cap					
7 day PY 9 mm GL (5.5 mm HL)	No trace	No trace	Early cap					
10 day PY 10.5 mm GL (6.5 mm HL)	Slight swelling of lamina	No trace	Early cap					
10 day PY 11 mm GL (7 mm HL)	Very early bud-like thickening	No trace	Middle cap					
14 day PY 13 mm GL (8 mm HL)	Late bud to early cap	No trace	Early to middle bell, flat successional lamina		Late bud			
14 day PY 13.5 mm GL (8 mm HL)	Early cap	Tiny bud-like thickening	Middle to late bell, flat successional lamina		Late bud			
15–16 day PY 14 mm GL (9 mm HL)	Early cap	No trace	Small, late bell, thin dentin, flat successional lamina	Early cap	Middle to late cap			
19 day PY 17 mm GL (10 mm HL)	Early bell	No trace	Moderately developed dentin, successional lamina mesially	Early bud- like swelling	Middle bell			
~19–20 day PY 16–17 mm GL	Early bell	No trace	Moderately developed dentin, successional lamina mesially	Early cap	Middle bell			
~19 day PY 16–18 mm GL	Late cap to early bell	No trace	Moderately thick dentin, thin enamel; successional lamina mesially	Late bud to early cap	Early to middle bell			

Stage	dP1	dP2	dP3	P3	M1	M2	M3	M4
25 day PY 20 mm GL (12.5 mm HL)	Middle to late bell	No trace	thick dentin, thin enamel; lingual successional lamina	Early to middle cap	Late bell, possible odontoblasts	Early cap		
~30–35 day PY ~23 mm GL	Late bell, very early dentin	No trace	Moderately thick dentin, thin enamel; lingual successional lamina	Late bell, early odontoblasts	Moderately developed dentin, thin enamel on metacone	Middle to late bell		
~35 day PY ~23–25 mm GL 13.5 mm HL	moderately thick dentin, moderately developed enamel	No trace	Moderately thick dentin, thin enamel; mesio-lingual successional lamina intact	Late bell, thin dentin	Moderately thick dentin, thin enamel on metacone	Middle to late bell		
~40–41 day PY ~29 mm GL 18 mm HL	Moderately thick dentin, moderately developed enamel	No trace	Moderately thick dentin, thin enamel; incomplete mesio-lingual successional lamina	Late bell, thin dentin	Moderately thick dentin and enamel on metacone	Late bell with thin dentin	Early to middle bud	

Note: GL, greatest length; HL, head length; PY, pouch young

Table 2. Development of *Dasyurus viverrinus* lower postcanine dentition

Stage	dp1	dp2	dp3	p3	m1	m2	m3	m4
30 hour PY 6 mm GL (3.25 mm HL)	No trace	No trace	Early bud-like thickening					
5–6 day PY 8 mm GL (4.5 mm HL)	No trace	No trace	Middle to late bud					
5–6 day PY 8.5 mm GL (4.5 mm HL)	No trace	No trace	Late bud to early cap					
6–7 day PY 9 mm GL (5 mm HL)	No trace	No trace	Late bud					
10 day PY 11 mm GL (7 mm HL)	Flattened early bud	No trace	Early to middle cap					
14 day PY 13 mm GL (8 mm HL)	Flattened late bud to early cap	Possible slight swelling	Middle bell, short flat successional lamina lingually		Early bud			

Stage	dp1	dp2	dp3	p3	m1	m2	m3	m4
~14 day PY 13.5 mm GL (8 mm HL)	Late bud to early cap	Slight swelling of dental lamina	Late bell, no odontoblasts, lingual successional lamina	Possible early bud-like swelling	Middle bud			
~15–16 day PY 14 mm GL (9 mm HL)	Early cap	Slight swelling of dental lamina	Small abnormal bell, moderately developed dentinal cap	No distinct bud-like swelling	Middle bell			
19 day PY 17 mm GL (10 mm HL)	Late cap to early bell	Slight swelling of dental lamina	Moderately developed dentin; mesio-lingual successional lamina	Possible early bud-like swelling	Middle to late bell			
~19–20 day PY 16–18 mm GL Bolk	Early bell	Possible slight swelling	Small, moderately thick dentinal arc, thin enamel	Early bud-like swelling at mesial end of dp3	Middle to late bell	Late cap		
25 day PY 20 mm GL (12.5 mm HL)	Middle bell	No trace	Small, thick dentin, thin enamel	Early bud	Late bell, thin to moderately developed dentin	Middle to late bell		
~30–35 day PY ~23 mm GL Bolk	Late bell, thin dentin	No trace	Small, abnormal dentinal mass, with thin enamel	Moderately sized, middle to late cap, mesial to abnormal dp3	Moderately thick dentin and moderately developed enamel on protoconid	Late bell, moderately developed dentin, thin enamel	Early bell	
~35 day PY 23–25 mm GL Bolk 13.5 mm HL	Late bell, moderately developed dentin, thin enamel	No trace	Abnormal, moderately thick dentinal arc with thin enamel	Moderately large, early to middle bell	Moderately thick dentin, moderately developed enamel on protoconid	Moderately thick dentin, thin enamel	Middle to late bell	
~40–41 day PY ~29 mm GL Bolk 18 mm HL	Moderately thick dentin, moderately developed enamel	No trace	Tiny, solid dentinal mass with thin enamel	Moderately large, late bell, possible odontoblasts	Thick dentin, moderately thick enamel on protoconid	Moderately thick dentin, moderately developed enamel on protoconid	Late bell, moderately developed dentin	Probable early bud

Note: GL, greatest length; HL, head length; PY, pouch young

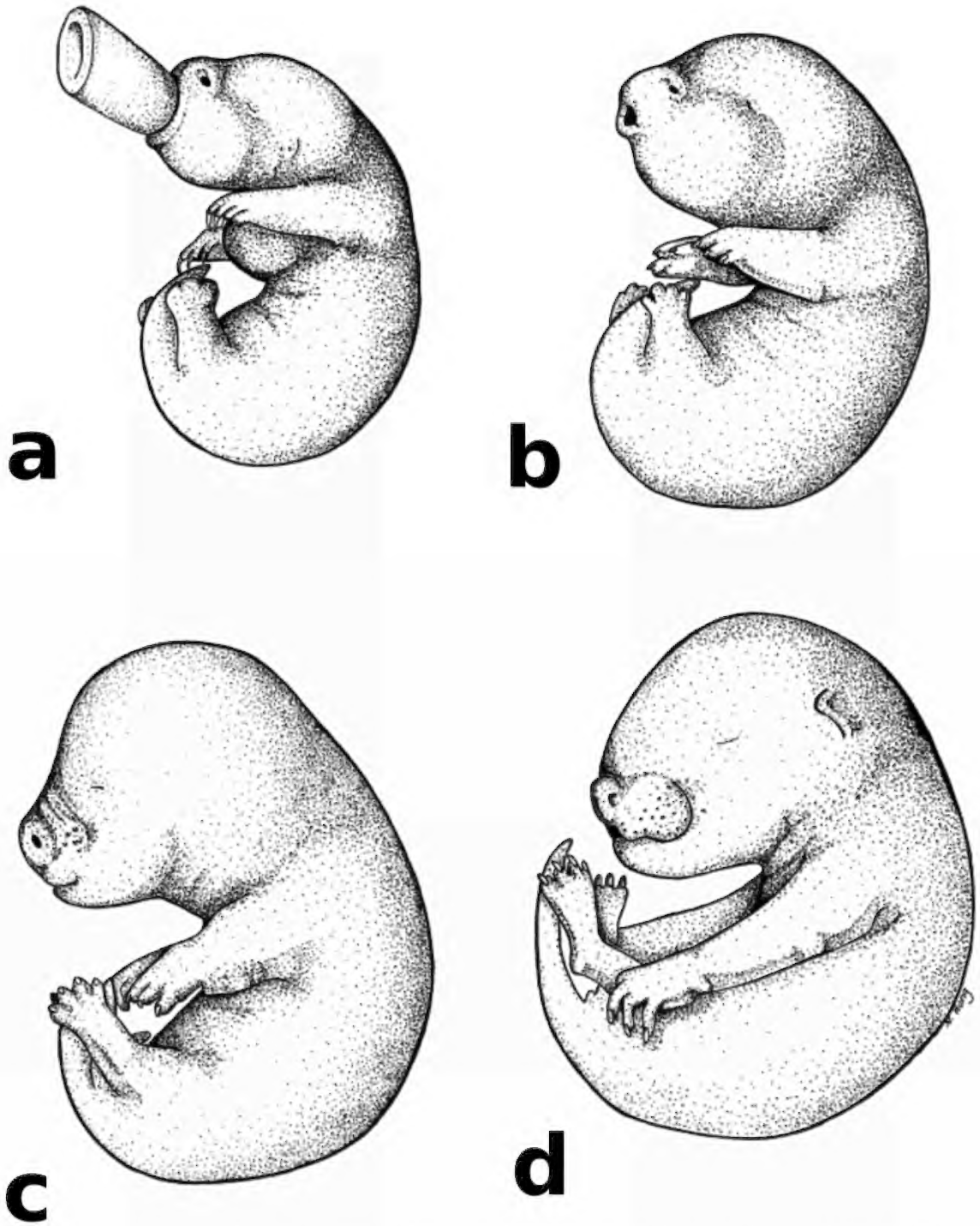

Figure 1. Four early pouch young of *Dasyurus viverrinus*: a, 30 hours old, 3.25 mm head length (HL); b, 5–6 days old, 4.5 mm HL; c, 14 days old, 8 mm HL; d, 25 days old, 12.5 mm HL.

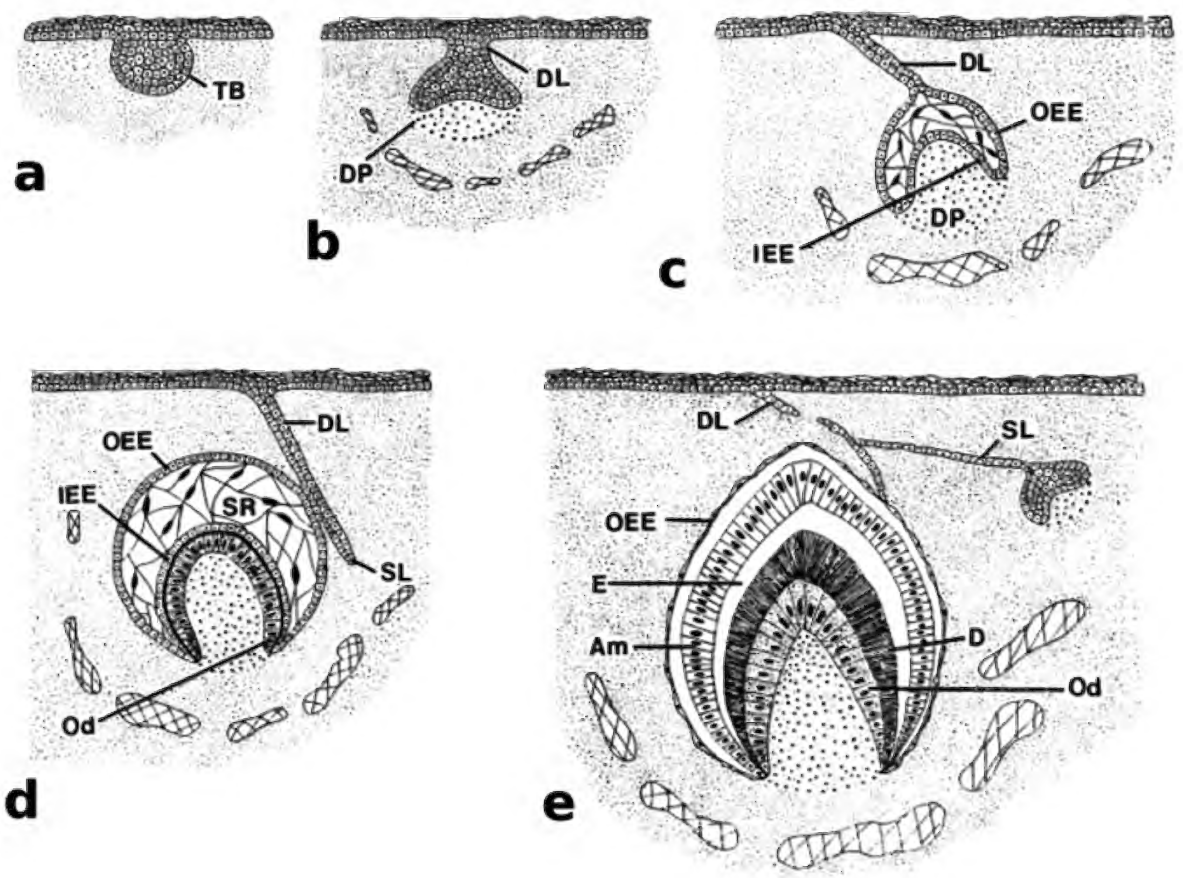

Figure 2. Transverse sections of early developmental stages of the dentition in marsupials: a, early tooth bud forming from the dental lamina; b, early-cap stage; c, middle-bell stage with elongate dental lamina; d, late-bell stage with odontoblasts and early lingual successional lamina; e, well-developed late-bell stage with dentin and enamel. A successional early-cap stage develops from the lingual successional lamina, showing early fragmentation of the dental lamina. Abbreviations: AM, ameloblasts; D, dentin; DL, dental lamina; DP, dental papilla; E, enamel; IEE, inner enamel epithelium; OD, odontoblasts; OEE, outer enamel epithelium; SL, successional lamina; SR, stellate reticulum; TB, tooth bud.

previously described in detail for marsupials (Luckett, 1993). The dental lamina was reduced distal to the developing canine. The lamina became thickened again distally at the level of the rostral end of the developing eye. It then gave rise to a moderate size early- to middle-bud stage dP3. The dental lamina and the maxillary bone disappeared distal to the dP3 bud.

In a slightly older embryo, 5–6 days old and measuring 8 mm GL and 4.5 mm HL (see fig. 7, Hill and Osman Hill, 1955, and our fig. 1b), three early developing incisors are now evident in the premaxillary region of the upper jaw. The anterior two incisors are moderately sized and flattened in the early- to middle-bud stages. The third incisor is moderately large and more spherical in the middle-bud stage, and is located nearer the distal end of the premaxilla. It has a smaller darkly stained buccal portion and a larger lingual lobular portion with lighter, normal-appearing cells. Based on its appearance in later developmental stages, these represent the buccal deciduous incisor and the more normal-appearing lingual successor incisor.

A moderately large late-bud to early-cap stage canine develops at the rostral extent of the maxilla. This also consists of a smaller darker buccal portion and a larger lingual paler-staining portion, representing the future deciduous and successor canines, respectively. The dental lamina is reduced distal to the developing canine and continues distally towards the level of the middle of the eye. At this region, the dental lamina enlarges and gives rise to a moderately large early-cap stage dP3, formed by invagination of the underlying dental papilla cells (see fig. 2b for an example). The dental lamina then disappears a short distance distal to this tooth, near the distal end of the eye.

In the lower jaw, three developing incisors are in early- to late-cap stages at the rostral extent of the dentary. The di1 is in a late-cap stage, with possible odontoblasts buccally and a lingual projection for an early successor bud for i1. The di2 has an early-cap stage buccally and a distolingual projecting lamina for a possible successor i2. The smaller di3 has a less distinct buccal early cap with a relatively indistinct lingual successional lamina. The moderately sized dc is in a late-bud stage with a lingual successional ridge. The dental lamina continues distally as a thin ridge with no suggestion of a dp1 or dp2. The dental lamina then thickens again distally, beneath the level of the distal portion of the eye, and gives rise to a moderately large late-bud to early-cap stage dp3. The dental lamina then ends distal to this developing tooth.

In a 10-day-old pouch young with a 6.5 mm HL and a 10–10.5 mm GL (see fig. 9 in Hill and Osman Hill, 1955), there is little change in the developing incisor and canine regions of the upper jaw. The dental lamina immediately distal to the canine exhibits a somewhat flattened early bud-like thickening for a possible primordium of dP1, but this is not very distinct. The dental lamina is then reduced and extends distally. At the level of the middle portion of the eye, the dental lamina thickens again and gives rise to a moderately large early-cap stage dP3. The dental lamina then ends distal to this tooth. In the lower jaw, there is also a moderately sized early-cap stage dp3 and no trace of a developing dp1.

In a slightly larger 10-day-old pouch young (7 mm HL and 11 mm GL), several distinct changes have occurred compared with the preceding specimen. The developing incisor region remains similar, whereas the deciduous canine has a tiny buccal nodule associated with a large distolingual projecting late-bud to early-cap stage successor canine in the upper jaw. Immediately following the canine is a tiny, somewhat flattened, probable early bud for dP1. The dental lamina is reduced distal to this early bud and extends distally to underlie the eye, where it enlarges to form a moderately sized middle-cap stage dP3. There was no distinct swelling of the dental lamina between the dP3 and the probable early-bud stage dP1. The dental lamina extends slightly distal to dP3 before it disappears.

Note that in the early developing pouch young, there is little space in the jaws for the developing anterior dentition, due in part to the greatly enlarged tongue and its intimate association with the large nipple (fig. 3). This often results in great compression and flattening of the more anterior developing teeth, whereas there is less compression distally in the region of the developing dP3 and molars.

In the lower jaw, there is also a small, flattened early-bud stage for dp1. The dental lamina is then reduced as it extends distally to form a moderately sized early- to middle-cap stage dp3. The dental lamina then ends distal to dp3. As in dasyurids with three premolars, the sequence of early development for the premolars in both jaws is dP3 > dP1 > dP2. As noted in this and later stages, it is the late-developing dP2 that is lost in both jaws of dasyurids with only two premolars.

In an older 14-day-old pouch young, with 8 mm HL and 13 mm GL (see fig. 10 in Hill and Osman Hill, 1955, and our fig. 1c), the developing relationships for dI1 and dI2 in the upper jaw were similar to those of the previous stage. In contrast, dI3 has an early cap knot enclosing a tiny dentinal arc. The small distolingual successional bud for I3 is still relatively small. A small buccal epithelial knot is evident for dC, and there is a large middle-bud stage successor for the canine that is associated with a deep maxillary alveolus. A small, flattened late-bud to early-cap dP1 follows the canine immediately, and then the dental lamina is reduced distal to this. There is a possible slight swelling of the dental lamina beneath the anterior end of the eye, but this is not very distinct. The dental lamina is then reduced distal to this slight swelling. The dental lamina enlarges further distally and gives rise to a moderately sized early- to middle-bell stage dP3 beneath the middle third of the eye (see fig. 2c for a middle-bell stage tooth). This tooth is still intact with its primary dental lamina origin. A flattened lingual successional lamina extends mesial to dP3. Distal to dP3 is a moderately sized late-bud stage M1 underlying the distal end of the large eye. The dental lamina ends distal to this tooth.

In the lower jaw, the di1 is small and cap like, enclosing thin distinct dentin. Distolingual to this is the larger early-bud stage successor i1. The di2 is also a small cap with an irregular dentinal fragment; a slightly larger successor i2 is placed distolingually in a late-bud to early-cap stage. The tiny di3 cap lacks dentin, and its distolingual successor ridge lacks a distinct successor tooth. The small, dark cap for dc lacks dentin and has a distolingual middle-bud stage successor canine. The small, flattened dp1 follows immediately and is in the late-bud to early-cap stage. There is no distinct evidence for a dp2 swelling. Somewhat more distally there is a small middle-bell stage dp3 with a short, flattened lingual successional lamina. Immediately distal to this tooth is a moderately sized early bud for m1. The dental lamina disappears distal to this developing tooth.

In a slightly larger 14-day-old pouch young (13.5 mm GL and 8 mm HL; see fig. 10 in Hill and Osman Hill, 1955), some notable changes are evident in the canine and postcanine dentition. The successor canine is now in the early- to middle-bell stage in the upper jaw. The tiny, flattened dP1 is in the early-cap stage. The dental lamina becomes reduced distal to this tooth and then enlarges slightly to form a possible primordium for a rudimentary dP2. However, the dental lamina is reduced distal to this slight swelling and then enlarges further distally and gives rise to a moderately large middle- to late-bell stage dP3. This tooth has moderately developed stellate reticulum, and a short, slender lingual successional lamina extends mesial to this tooth (see fig. 2d for a late-bell stage with a lingual successional lamina). The dP3 lies beneath the middle region of the eye. The primary dental lamina extends distal to dP3 and gives rise to a moderately large late-bud M1 beneath the distal region of the eye. The dental lamina then disappears distal to this bud.

In the lower jaw, the successor canine is now in the late-bud to early-cap stage. This is followed immediately by the small, elongate late-bud to early-cap stage dp1. The dental lamina is slightly swollen distal to this tooth, but this is not very significant. Further distally, the small dp3 is in the late-bell stage with moderately developed stellate reticulum but no

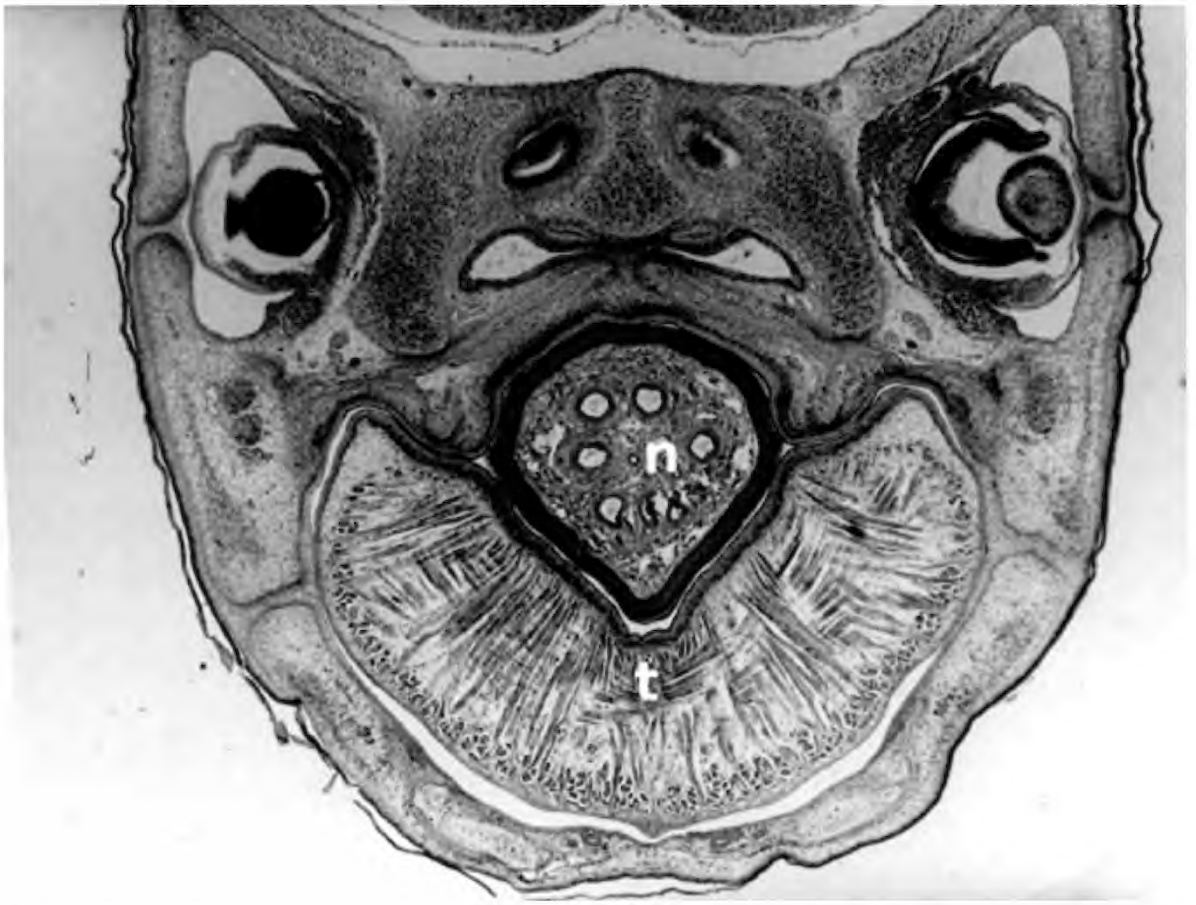

Figure 3. Transverse section through the head at the level of the developing eyes in a 10-day-old *Dasyurus viverrinus* embryo (7 mm head length). Note the close compression between the large tongue (T) and the nipple (N). No developing teeth are evident.

dentin. There is a lingual successional lamina that extends mesial to dp3 and terminates with a slight bud-like swelling. Distal to dp3 is a large middle-bud stage m1, and then the dental lamina disappears distal to this.

In a slightly older pouch young (13–15 mm GL and 9 mm HL) estimated to be 15–16 days old, a significant change has occurred in the postcanine region of the upper jaw. The small dP1 is in the early-cap stage and the dental lamina is greatly reduced distal to this tooth without any suggestion of a swelling for a rudimentary dP2. Further distally, the small to moderate sized dP3 is in the late-bell stage with thin dentin on its apex. The tooth is relatively superficial with a short, intact primary dental lamina stalk to the oral epithelium. The tooth lies beneath the anterior ⅓ of the eye. The slender lingual successional lamina extends mesial to the tooth and then enlarges to form a moderately sized early-cap stage successor P3. The successor P3 extends mesially beneath the anterior margin of the eye. Distal to this, a moderately large middle- to late-cap stage M1 develops beneath the level of the middle of the eye. The dental lamina then disappears distal to this tooth.

In the lower jaw, the dp1 is a moderately sized early-cap stage. The dental lamina is reduced distal to this tooth; there is a slight swelling distally, but this is not very distinct. Further distally, the dental lamina enlarges again and gives rise to a small to moderately sized, somewhat abnormal dp3 with an irregular, moderately developed dentinal cap. There is a short, primary dental lamina stalk to the oral epithelium. The tooth is in a shallow bony alveolus and has a flattened lingual successional lamina. Distal to this tooth is a large middle-bell stage m1. The dental lamina disappears distal to the developing molar. In both jaws, the dP3 appear to be relatively smaller than in earlier stages and they lie closer to the oral epithelium.

In the later developmental stages, we will only discuss the postcanine development of the *Dasyurus* pouch young because there is little controversy concerning the development of the incisor and canine regions. In a 19-day-old pouch young (17 mm GL and 10 mm HL; see fig. 11 in Hill and Osman

Hill, 1955), the small dP1 is somewhat flattened or compressed and has now attained the early-bell stage in the upper jaw. The dental lamina is reduced distal to this tooth and becomes detached from the oral epithelium. The dental lamina becomes reattached further distally and forms an early bud-like swelling; this possibly represents the rudiment of a dP2. The dental lamina is then reduced again and extends further distally; it then enlarges to form a small late-bell stage dP3. There is moderately developed dentin but no enamel on this small tooth. It lies beneath the middle of the eye in a shallow bony alveolus. A lingual successional lamina extends mesially from dP3 and forms a slight bud-like thickening. As noted in the later developmental stages, this thickening is the primordium for the later developing successor P3. The dental lamina extends distal to dP3 and then enlarges to form a moderately large middle-bell stage M1. This tooth lies beneath the distal half of the eye; the dental lamina disappears distal to this tooth.

In the lower jaw, dp1 is a moderately sized, late-cap to early-bell stage tooth with a shallow bony alveolus. The dental lamina is slightly swollen distal to this tooth (possibly representing the site of the lost dp2); then further distally, the dental lamina thickens again and gives rise to a small late-bell stage dp3 with a moderately developed layer of dentin. The lingual successional lamina of this tooth extends mesially, where it is slightly thickened terminally. The dental lamina extends distal to this tooth and gives rise to a large middle- to late-bell stage m1. The dental lamina disappears distal to this tooth.

In a later pouch young of 19–20 days old (16–18 mm GL), sectioned by Dr Louis Bolk, the dP1 is a small tooth in the late-cap to early-bell stage in the upper jaw. The dental lamina distal to this tooth is detached from the oral epithelium. There is no trace of a possible rudimentary dP2. Further distally, the dental lamina reappears and gives rise to a small, late-bell stage dP3 with moderately thick dentin and a thin film of early enamel. The lingual successional lamina of dP3 extends mesially and gives rise to a small late-bud to early-cap stage successor P3, which lies anterior to dP3 (see fig. 2e for a late-bell stage dP3 and its successor early-cap stage P3). Distal to dP3, the dental lamina gives rise to a moderately large early- to middle-bell stage M1. The dental lamina then disappears distal to this tooth.

In the lower jaw, the moderately sized dp1 is in the early-bell stage. The tooth is somewhat compressed and lies in a shallow bony alveolus. There is only a slight possible swelling of the dental lamina distal to this tooth in the region of the missing dp2. Further distally, the dental lamina thickens again and gives rise to a small late-bell stage dp3 with a moderately thick arc of dentin. There is also a thin layer of darkly stained enamel. The slender lingual successional lamina adjacent to dp3 extends mesially and is enlarged as a slight early bud-like swelling for the future successional p3. The dental lamina is reduced distal to dp3 and then enlarges again to form a large middle- to late-bell stage m1. Distal to this tooth is a moderately large late-cap stage for m2. The dental lamina disappears distal to this tooth.

In another 19–20-day-old pouch young (10 mm HL and 16–17 mm GL), there are slight advancements for some of the developing teeth. A moderately sized dP1 is in the early-bell stage in the upper jaw. There is no distinct evidence for a rudimentary dP2 swelling distal to this tooth. The dental lamina thickens further distally and gives rise to a small to moderately sized late-bell stage dP3 with moderately developed dentin on its crown. There is a shallow bony alveolus for the tooth, which lies beneath the anterior third of the eye. The lingual successional lamina of dP3 extends mesially and thickens to give rise to a small early-cap stage successor P3. Distal to the dP3, the dental lamina thickens again and gives rise to a moderately large middle-bell stage M1. This tooth is positioned beneath the middle of the eye. The dental lamina thins and then disappears distal to M1.

In the lower jaw, a moderately sized dp1 is in the late-cap to early-bell stage. There is no distinct evidence for a rudimentary dp2 distal to this tooth. Further distally, there is a small, somewhat abnormal dp3 with a moderately developed dentinal arc but no stellate reticulum. The lingual successional lamina of dp3 is slightly thickened mesially and then gives rise to a small middle-bud stage successor p3 further anteriorly. Distal to dp3, the dental lamina enlarges and gives origin to a large middle- to late-bell stage m1. Distal to this tooth, the dental lamina gives rise to a moderately sized late-cap stage m2. The dental lamina then disappears distal to this tooth. Note that in the 19–20-day-old pouch young, the dentition in the lower jaw is accelerated in its development compared with that in the upper jaw; this trend continues to increase in later developmental stages.

In a later 25-day-old pouch young (20 mm GL and 12.5 mm HL; see fig. 12 in Hill and Osman Hill, 1955, and our fig. 1d) that has been sectioned longitudinally, dP1 is a small to moderately sized tooth in the middle- to late-bell stage in the upper jaw (fig. 4). As in the previous stage, there is no suggestion of a dP2 rudiment. Further distally, the small to moderately sized dP3 has relatively thick dentin and thin enamel. The tooth is located beneath the anterior ⅓ of the eye. The lingual successional lamina of dP3 extends mesially and thickens to form a moderately large early to middle-cap stage successor P3. The deciduous and successor P3 appear to arise from a common primary dental lamina stalk. This is due to the partial fragmentation of the primary dental lamina stalk in later stages of development (compare fig. 4 with 2e). Distal to the developing dP3/P3 complex, the M1 is now in a large late-bell stage with possible early odontoblasts but no dentin. This tooth underlies the middle of the eye. A moderately sized early-cap stage M2 develops distal to M1. The dental lamina then disappears distal to this tooth.

In the lower jaw, dp1 is now a moderately large middle-bell stage tooth, developing immediately distal to the large developing canine. There is no distinct evidence for a rudiment of dp2. Further distally, the small to moderately sized dp3 is partially covered with a thick layer of dentin and a thin layer of enamel. Mesiolingual to the small dp3, the lingual successional lamina gives rise to a larger early-bud stage p3. Further distally is a large late-bell stage m1 with moderately developed dentin on the apex of the tall protoconid. Distal to this tooth, the dental lamina gives rise to a large middle- to late-bell stage m2. A possible early bud for m3 lies distal to this tooth, but problems with the tissue make it difficult to be certain of this.

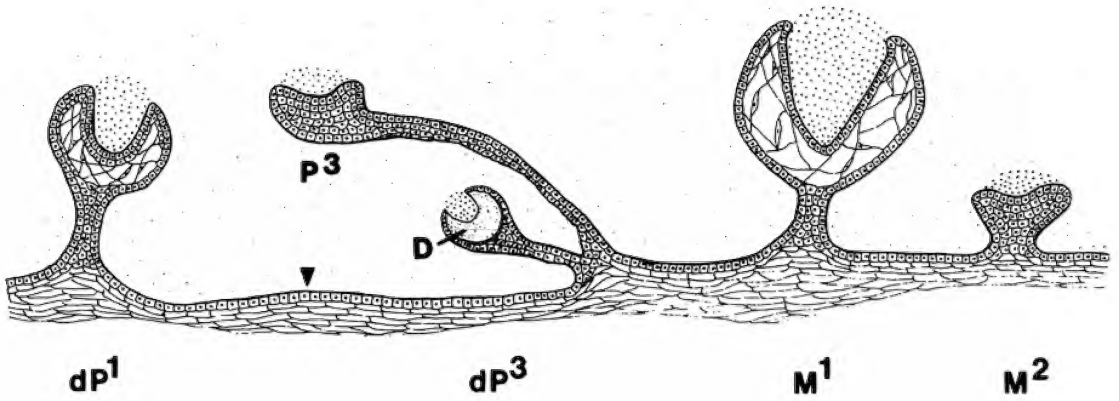

Figure 4. Parasagittal section through the dentition in a 25-day-old pouch young (12.5 mm head length) showing the developing teeth between dP1 and M2 in the upper jaw. Arrowhead refers to the site of the missing dP2. Abbreviation: D, location of developing dP3 follicle.

In a 30–35-day-old pouch young (23–24 mm GL and 13.5 mm HL; see fig. 13 in Hill and Osman Hill, 1955), the dP1 is now a moderately sized tooth with moderately thick dentin and thin to moderately developed enamel on its crown in the upper jaw. The tooth lies in a shallow bony alveolus, just below the oral epithelium. This is related in part due to the large canine that partially underlies the smaller dP1 throughout its length. There is no trace of a rudimentary dP2. Further distally, the dental lamina thickens and gives rise to a small, somewhat elongate dP3 with moderately thick dentin and a partially disrupted layer of enamel. The tooth lies anterior to the developing eye. The lingual successional lamina of dP3 extends mesially and gives rise to a larger moderately sized late-bell stage successor P3 with odontoblasts and a thin layer of predentin on its crown. The P3 extends both anterior and posterior to dP3 because of its larger size. There is a normally sized developing bony alveolus for P3, whereas a distinct bony alveolus is lacking for the small dP3. Instead, the small deciduous tooth lies more superficially, in the apex of the deeper alveolus for the larger P3. Distal to the dP3/P3 complex, the large M1 has moderately thick dentin and thin enamel on its elevated metacone. There is a flattened residual lingual lamina along the extent of the tooth. This tooth lies beneath the anterior half of the eye. A moderately large middle- to late-bell stage M2 lies beneath the distal half of the eye. The dental lamina disappears distal to this tooth.

In the lower jaw, dp1 is a relatively large tooth with moderately developed dentin and thin enamel on its apex. There is no suggestion of a rudimentary dp2. Further distally, the small dp3 has a relatively thick dentinal arc overlain by a thin film of enamel. The enamel is covered by inactive cuboidal ameloblasts. Lingual to the small abnormal dp3 is a thin successional lamina; this extends further mesially and gives rise to a moderately large early- to middle-bell stage p3 with a loosening of its stellate reticulum. Distal to the dp3/p3 complex, the m1 is a large tooth with moderately thick dentin and thin to moderately developed enamel on the apex of its tall protoconid. The tooth has a short, flat residual lamina. Distal to this tooth is a large m2, also with moderately developed to moderately thick dentin and thin enamel on its tall protoconid. The m2 also has a short, flat residual lamina. A moderately large m3 lies distal to m2 and is in the middle- to late-bell stage. The dental lamina disappears distal to this tooth.

Another pouch young 30–35 days old (23 mm GL) was sectioned by Louis Bolk and showed some small differences with the previous specimen. The dP1 is small to moderately sized and is in the late-bell stage with early odontoblasts and thin predentin in the upper jaw. The dp1 has a short, flat lingual successional lamina. Again, there is no suggestion of a rudimentary dP2. The small, somewhat abnormal dP3 has moderately thick dentin and possibly a thin film of enamel. Mesio-lingual to dP3 is a moderately sized late-bell stage P3 with very early odontoblasts. The elongate lingual successional lamina is fragmented in places and it is not clearly connected to dP3, in contrast to earlier stages. Distal to dP3 is a large late-bell stage M1 with moderately developed dentin and thin enamel on the tall metacone. A prominent, flattened residual lamina is present lingually. Distal to this tooth is a moderately large middle- to late-bell stage M2. The dental lamina disappears distal to this tooth.

In the lower jaw, the moderately large late-bell stage dp1 has thin predentin on the apex of its single cusp; it immediately follows the large canine. There is no suggestion of a rudimentary dp2. Further distally is a small, abnormal dentinal mass for the rudimentary dp3 with a thin layer of enamel on the surface of the dentin. The primary dental lamina connection to the oral epithelium persists. Anterior to the abnormal dp3 is a moderately sized middle- to late-cap stage p3. Only a few fragmented epithelial nodules represent

the earlier remnants of the lingual successional lamina from dp3. Distal to dp3 is the large m1 with moderately thick dentin and thin to moderately developed enamel on the apex of its tall protoconid. A thin, flattened residual lamina is evident mesially. Distal to this is a large late-bell stage m2 with moderately developed dentin and thin enamel on the apex of the tall protoconid. There is also a prominent, short residual lamina lingually. Distal to this tooth is a moderately sized early-bell stage m3; the dental lamina then disappears distal to this tooth.

In a later pouch young of about 41 days old (29 mm GL and 18 mm HL; see fig. 14 in Hill and Osman Hill, 1955), also sectioned by Louis Bolk, further changes occurred, especially with regards to the dP3 and P3 in both jaws. In the upper jaw, the small dP1 now has moderately thick dentin and moderately developed enamel on the apex of the unicuspid tooth. There is a short, flattened lingual successional lamina, and again no trace of a rudimentary dP2. Further distally, there is a small dP3 with moderately thick dentin and moderately developed enamel. Ameloblasts are low cuboidal and probably are no longer functional. Fragmented strands of the lingual successional lamina extend anteriorly and give rise to a moderately sized late-bell stage successor P3 with thin early predentin on its apex. Further distally, the large M1 appears; it has moderately thick dentin and enamel on its tall disto-buccal metacone. Distal to this tooth is a large late-bell stage M2. This tooth also has an elevated disto-buccal cusp that has odontoblasts and a very thin layer of predentin. Following this tooth is a moderately sized early to middle-bud stage M3. The dental lamina then disappears distal to this developing tooth.

In the lower jaw, dp1 is a moderately sized tooth with a relatively thick layer of dentin and a moderately developed layer of enamel (partially disrupted). Its primary dental lamina stalk is still attached to the oral epithelium. Only a slight suggestion of the thin lingual successional lamina is evident mesially. There is no trace of a rudimentary dp2. Distal to dp1 is a very small, abnormal dp3 with a prominent dentinal mass. There is also a very thin film of enamel, although there are no distinct remnants of ameloblasts. The tooth is considerably reduced in size compared with earlier developmental stages. The primary dental lamina connection of dp3 with the oral epithelium and its lingual successional lamina are also broken in places. Nevertheless, the fragmented lingual successional lamina extends mesially and gives rise to a moderately large late-bell stage successor p3. The p3 has well-developed stellate reticulum and possibly early odontoblasts, although this is not clear. The tiny dp3 lies more superficial than its larger successor and lacks a distinct bony alveolus.

Distal to dp3 is a large m1 with thick dentin and moderately thick enamel on its tall, mesio to buccal protoconid. The tooth lies in a deep bony alveolus. Distal to m1 is a large m2 with moderately thick dentin and moderately developed enamel on its tall protoconid. Further distally, m3 is a moderately large tooth in the late-bell stage with a moderately developed layer of dentin on its tall protoconid. There are also early ameloblasts on the tooth cusp, but no enamel. There is a well-developed lingual residual lamina mesially on the tooth. Distal to this tooth is a possible early bud for m4 developing on both sides of the jaw, but tissue disruption makes this difficult to confirm. The dental lamina disappears distal to this region.

Later development and eruption of the dentition in *Dasyurus viverrinus*

We would like to have been able to microscopically examine later developmental stages of the dentition in *Dasyurus viverrinus*, but at the time we were working at the Hubrecht Laboratory of Comparative Embryology, later stages were not available. Many older specimens, from 46 days old to about 120 days old, were described by Hill and Osman Hill (1955), but only a few brief comments were provided by them concerning the early eruption of a few teeth. Presumably, these later stages of alcohol specimens were included in the Hill collection when it was moved with the Hubrecht collection to the Museum für Naturkunde.

Concerning the later development and eruption of teeth in *Dasyurus viverrinus*, Hill and Osman Hill (1955) cited the earlier studies by Thomas (1887) and especially Woodward (1896), and accepted their beliefs that P3 is the tooth that has been suppressed in this species with two premolars. They all agreed that a vestigial dP3 developed in the jaws and that the lingual successional lamina of this tooth was much swollen and probably represented a rudiment for the successor P3, although it probably does not develop much further. All agreed that the vestigial dP3 is present but does not erupt and that the swollen primordium of P3 does not differentiate much further or erupt.

It seems clear to us that none of these authors microscopically examined later developmental stages of *Dasyurus viverrinus* beyond the "much swollen" stage of P3. In our studies, this stage occurred at 15–20 days of development. Indeed, in some 19–20-day-old pouch young, the successor P3 was already in the late-bud to early-cap stage. Between 20 and 41 days of development in our study, the P3 developed normally in both jaws, attaining the late-bell stage. In contrast, the dP3 in both jaws became relatively smaller and more abnormal in these later developmental stages; this would be consistent with continued reduction and non-eruption of dP3 in later stages.

The absence of a developing dP2 and the normal development of the successor P3 in the 25–41-day-old pouch young in our study provide a strong basis for our belief that dP1 and P3 are the two erupting premolars in both jaws of later developmental stages in *Dasyurus viverrinus*. Hopefully, future investigators will microscopically examine the later developmental stages and early eruption of the jaws in *Dasyurus viverrinus* to corroborate (or refute) our hypothesis of dental homologies.

Comparison of *Dasyurus viverrinus* with the three-premolared dasyurids *Sminthopsis virginiae* (Luckett and Woolley, 1996) and *Antechinus stuartii* (Luckett and Hong Luckett, pers obs) shows that there is a similar pattern in the early postcanine development of the premolars in these two groups, despite the loss of one deciduous premolar in the *Dasyurus* species. While the deciduous premolars differentiate

and develop in a posterior to anterior series (dP3 > dP2 > dP1) in both jaws of the didelphids *Didelphis* and *Monodelphis*, the dasyurids show a different developmental sequence of dP3 > dP1 > dP2. In *Sminthopsis virginiae*, a previous study showed that dP2 was relatively late in its initiation, not appearing until about 20 days of pouch young development (Luckett and Woolley, 1996). The same is true for *Antechinus stuartii*. As shown in our developmental series of *Dasyurus viverrinus*, it is this later developing dP2 that has been lost in this species with only two premolars. In our *Dasyurus viverrinus* series, it was during the 15 to 20 days of development that there was a slight suggestion of thickening of the dental lamina between dP1 and dP3; this probably represented a rudimentary attempt to develop a dP2. In the later stages of development, from 25 to 41 days, there was no longer any sign of a rudimentary dP2.

Another interesting and unusual condition in *Dasyurus viverrinus*, when compared with the dasyurids with three premolars, is the nature of the development of dP3 in both jaws. The dP3 is the first postcanine tooth to initiate differentiation in both jaws, as also occurs in all three-premolared dasyurids examined, as well as in didelphids. In contrast with these marsupials with three premolars, however, the dP3 in *Dasyurus* undergoes an abnormal state of development in later stages in both jaws, including a relative reduction in size and having a relative superficial position in the jaw with only minimal development of a bony alveolus. This abnormal development of dP3 is even more noticeable in the lower jaw. There is a large amount of dentin but only minimal amounts of enamel. In contrast, the successional P3 is developing normally in both jaws and it is quickly larger in size and deeper in the jaw than its deciduous predecessor. Although we could not follow later stages histologically, it is the normal developing successor P3 that erupts adjacent to dP1 in both jaws. In contrast, we are unaware of any evidence for eruption of the small, abnormal dP3 in *Dasyurus viverrinus.*

Another significant difference between *Dasyurus viverrinus* and the dasyurids with three premolars is the accelerated rate of development and eruption of P3 in *Dasyurus*, when compared with these other dasyurids and with didelphids. In the 97-day-old *Sminthopsis virginiae* examined by us (see Luckett and Woolley, 1996), M1-2 are erupted in both jaws and M3 is partially (⅓) erupted in the upper jaw. In the lower jaw, m3 is almost completely erupted and the protoconid of m4 is in an early stage of eruption. The dP1 to dP3 are erupted in both jaws, whereas the moderately large and well-developed successor P3 is still unerupted in both jaws.

In contrast, there is no sign of an erupted or unerupted dP3 in either jaw of *Dasyurus viverrinus* at about 95 days old, and dP1 is in early eruption. The successor P3 is in early eruption at about 98 days old; this is about the same time as the early eruption of M1. These data on *Dasyurus viverrinus* eruption are from the study by Merchant et al. (1984), although we have changed the names of their premolars ("first and second upper premolars") to correspond to our more precise and correct terminology because they considered dP2 to be present and P3 to be lost. As with most other studies on *Dasyurus viverrinus*, Merchant et al. (1984) did not microscopically examine any of their extensive series of developing pouch young. We also note that these authors found no trace of an erupted dP3 in earlier or later stages of development; this is consistent with our findings of abnormal development of dP3 in later stages of development.

Variation in the fate of dP3 within *Dasyurus*

Neither Hill and Osman Hill (1955) nor Merchant et al. (1984) could detect any evidence for the eruption of a rudimentary dP3 in *Dasyurus viverrinus*, and we have not seen such a tooth in any of the juvenile or subadult skulls that we have examined. However, in another *Dasyurus* species that we have studied, *Dasyurus albopunctatus*, we have noted similar developmental stages to those of *Dasyurus viverrinus*, as well as an unusual condition during later developmental stages and early eruption (Luckett pers obs). Our specimens of *Dasyurus albopunctatus* consist of microscopic sections of two early pouch young and a larger number (26) of skulls of juvenile and subadult specimens with erupting postcanine dentitions.

In the youngest specimen (fig. 5) that we examined microscopically (AMNH 195149; 12 mm HL), the postcanine region contained a moderately large late-bell stage dP1 with no

Figure 5. *Dasyurus albopunctatus* pouch young (AMNH 195149, 12 mm head length). Scale bar is 5 mm.

odontoblasts in the upper jaw. There was a diastema for the missing dP2 with no swelling of the dental lamina. Further distally was a moderately sized dP3 with moderately thick dentin and moderately developed enamel. Extending mesially from the dP3 was a lingual successional lamina that gave rise to an early- to middle-bud stage successional P3. Further distally was a large M1 with moderately developed dentin but no enamel. Distal to this was an early- to middle-cap stage for M2; the dental lamina ended distal to this tooth. This specimen is very similar in its developmental features to that of our *Dasyurus viverrinus* 25-day-old pouch young (12.5 mm HL). A later developmental stage of *Dasyurus albopunctatus* (AMNH 193967; 32 mm HL) was considerably advanced. The dP1 had thick dentin and enamel, and again, there was no trace of a rudimentary dP2 in the upper jaw. The now tiny calcified dP3 was elongate and slender, considerably reduced in relative size compared with the previous specimen; it was very close to the overlying alveolar margins. Deeper in the jaw and lingual to this was a moderately large successor P3, with thick dentin and enamel. This specimen was considerably more advanced in its development compared with our 41-day-old *Dasyurus viverrinus*.

In a slightly later juvenile skull of *Dasyurus albopunctatus* (AM M24313; skull damaged; not measured), the second to fourth incisors were in early eruption in the upper jaw and the canine was in an earlier stage of eruption. The dP1 was ½–⅔ erupted and there was no trace of a dP2. Immediately distal to this, the moderately sized successor P3 was in very early eruption, less than that of dP1. Lying on the apex of the P3 crown was a tiny, elongate and pearl-shaped dP3 on both sides of the jaw. The tiny dP3 had a crown height of 1.3 mm on the right side and 1.4 mm on the left side. The M1 was almost completely erupted and M2 was in early eruption. In comparison with the data on *Dasyurus viverrinus* from Merchant et al. (1984), this specimen would be 95–98 days old. In the lower jaw, the incisors are almost completely erupted, as is the canine. The dp1 is also almost completely erupted. The successor p3 is about ⅔ erupted and there is no trace of a tiny dp3. The m1 is almost completely erupted and m2 is about ½ erupted.

In nine juvenile skulls of *Dasyurus albopunctatus* from later developmental stages that we examined, we could see the tiny dP3 lying adjacent to the erupting P3 in the upper jaw in skulls where the P3 was not completely erupted (see fig 6a–d). It would be incorrect to say that the tiny dP3 were erupted, and we prefer to consider them to be *displaced* during the eruption of P3. The oldest specimen that we examined with the tiny dP3 was a partially damaged juvenile skull (AMNH 151980; 43.51 mm Skull Length). The dP1 was erupted and P3 was almost completely erupted on the right side of the upper jaw. The M1 was erupted and M2 was almost completely erupted. In the lower jaw, dp1, p3 m1 and m2 were erupted and m3 was about ¾ erupted. As in all the juvenile specimens examined by us for this species, there was no trace of a dp3 in the lower jaw. This specimen was briefly noted by Tate (1947, p. 142) who stated that the "upper and lower fourth premolars are absent. The milk P4, however, can still be detected". As we have shown in this and earlier developmental stages, it is dP2 that is the missing tooth in both jaws, and P3 (his fourth premolars) is developed in both jaws. It was the tiny dP3 (his "milk P4") that he detected in the upper jaw.

In later developmental stages of *Dasyurus albopunctatus*, in which P3 was completely or almost completely erupted in the upper jaw, the tiny dP3 was absent in most cases. However, in a few instances of some specimens with P3 erupted, tiny tooth-like fragments of a probable apical or basal remnant of dP3 were found unilaterally (AMNH 151973, 151971). The oldest juvenile that we found with a slender root remnant of dP3 unilaterally (fig. 6d) was in a male (BBM-NG 97868; 47.25 mm Skull Length) with dP1, P3, M1 and M2 erupted in the upper jaw, and M3 was about ½ erupted.

We suggest that the pattern of dental development and eruption in *Dasyurus albopunctatus* is an intermediate condition between that of the dasyurids with three premolars that we have examined and *Dasyurus viverrinus*. Both of our species of *Dasyurus* have a similar accelerated rate of development for the eruption of P3 at about the same time as M1 and M2, compared with that for the dasyurid species *Sminthopsis* and *Antechinus* with three premolars. The greatly reduced dP3 adjacent to the erupting P3 in the upper jaw of *Dasyurus albopunctatus* is an intermediate condition between the presence of an erupted dP3 in the dasyurids with three premolars and its absence in *Dasyurus viverrinus*.

Although we have not made an extensive search for rudimentary dP3 remnants in other species of *Dasyurus*, we suspect that they can and will be found in some of these species. We have seen one such probable tiny dP3 in *Dasyurus geoffroii* and *Dasyurus hallucatus*, and we have seen a similar condition of accelerated eruption of P3 in these two species. We also note that Archer (1975, p. 255) reported the presence of a rudimentary spicule-like tooth in the position of the "normally absent" dP3 in *Dasyurus geoffroii* (WAM M6370); we suspect this was also a dP3 fragment.

A final thought. Although *Dasyurus viverrinus* is considered to be extinct on mainland Australia, we hope that investigators in Tasmania will help complete our studies on the later development and eruption of the dentition in this species, which still exists there but is threatened. Investigators there have studied many other aspects of the biology of this interesting species, and we hope that this paper will stimulate some to further support or challenge our findings on dental development.

Acknowledgements

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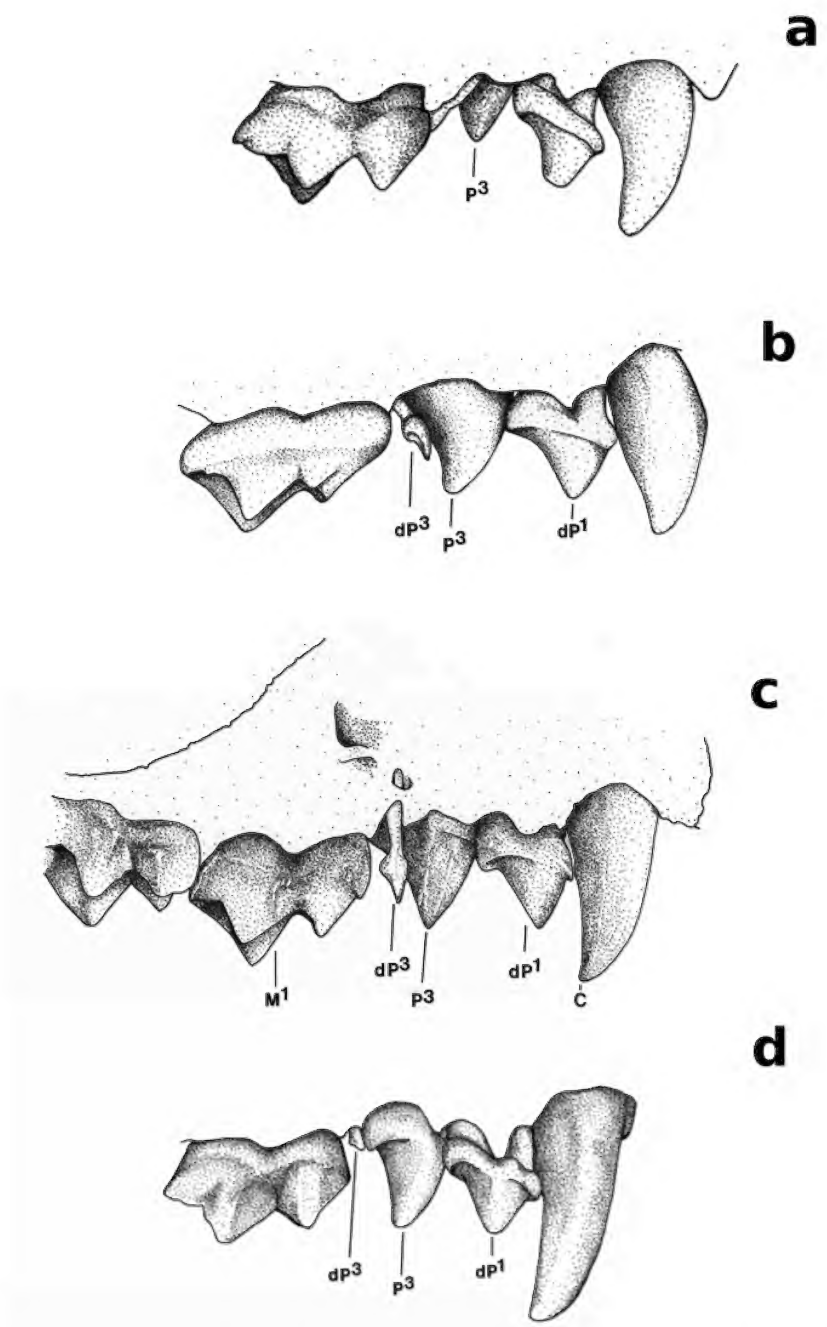

Figure 6. *Dasyurus albopunctatus* pouch young: a, (AMNH 190927; 36.64 mm skull length). Erupting teeth in the upper jaw with canine about ½ erupted. The dP1 is almost completely erupted and P3 is in early eruption. A tiny, slender dP3 is lying on the distal margins of the erupting P3, pointing posteriorly; its apex is not evident. M1 is erupted and the M2 is about ¾ erupting (not shown); b, (AMNH 221650; 37.53 mm skull length) slightly older than the preceding. The dP1 is erupted in the upper jaw and P3 is erupting (½–⅔). A tiny, elongate dP3 is evident along the posterior margins of the erupting P3; c, (BBM – NG 28247; 37.89 mm skull length). The dP1 is erupted, and the P3 is almost completely erupted in the upper jaw. A tiny, slender and elongate dP3 is evident along the distal margin of P3 and its root extends distally beneath the anterior opening of the infraorbital canal; d, (BBM – NG 97868; 47.25 mm skull length). In this older young, the P3 is almost completely erupted in the upper jaw. A tiny, slender root remnant of dP3 is evident, distal to the buccal end of P3.

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A review of the Australasian genus *Pseudophycis* (Gadiformes: Moridae), redescribing its four species and resurrecting the name *Physiculus palmatus* Klunzinger, 1872, for the Australian Red Cod

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Abstract

Gomon, M.F., Struthers, C.D. and Kemp, J. 2021. A review of the Australasian genus *Pseudophycis* (Gadiformes: Moridae), redescribing its four species and resurrecting the name *Physiculus palmatus* Klunzinger, 1872, for the Australian Red Cod. *Memoirs of Museum Victoria* 80: 59–99.

The commercially fished Red Cod *Pseudophycis bachus* Forster in Bloch and Schneider, 1801, is shown on the basis of both morphological and genetic evidence to be confined to New Zealand waters. The separation of the closely related but distinct Australian cognate brings the number of species in the Australasian genus *Pseudophycis* to four. The name *Physiculus palmatus* Klunzinger, 1872, which was long thought to be a junior synonym of *Pseudophycis barbata* Günther, 1862, is demonstrated to have been originally proposed for the Australian endemic. *Pseudophycis palmata* (new combination) differs from *P. bachus* in having a prominent black blotch or spot basally on the pectoral fin that does not extend dorsally onto the body, in contrast to distinctly extending onto body, the second dorsal fin with 47–56 rather than 40–45 rays, the anal fin with 50–57 rather than 42–48 rays and the vertebral column with 47–50 rather than 44–46 total vertebrae. Diagnoses, colour descriptions, images and distributions for all four species and a key to members of the genus are provided.

Keywords

Teleostei, Actinopterygii, morphology, re-description, comparison, distribution, CO1

Introduction

In an annotated catalogue of gadiform fishes of the world, Cohen et al. (1990) treated the morid genus *Pseudophycis* as comprising three species: *Pseudophycis bachus* Forster in Bloch and Schneider, 1801, *P. barbata* Günther, 1863, and *P. breviuscula* Richardson, 1846, all confined to the temperate waters of New Zealand and Australia. The taxonomy followed Paulin's (1983) review of New Zealand species of Moridae that concluded that only three are present in New Zealand and Australian waters, despite the historical confusion over which names apply to the various *Pseudophycis* species. Paulin did, however, observe meristic variations in fin ray and scale counts between New Zealand specimens and the limited number of Australian specimens of *P. bachus* at his disposal, saying "examination of a larger sample of Australian specimens might show some differences but, in view of the variability within species of Moridae, there would probably be little justification for separating the populations at the species level" (Paulin, 1983, p. 92). Subsequent authors (e.g. Gomon in Gomon et al., 1994; Kuiter, 1993; Last et al., 1983; Paxton and Hanley in Paxton et al., 1989; Paxton et al., 2006; Yearsley et al., 1999) dealing with temperate Australian fish biodiversity followed Paulin (1983) and Cohen et al. (1990) in treating the Australian Red Cod as conspecific with the New Zealand species.

Smith et al. (2008) detected genetic differences between Australasian samples of *Pseudophycis* using the CO1 locus. Their work included eight samples of *P. bachus*, four each from Australia and New Zealand, six samples of *P. barbata* from Australia, but no samples of the third species, *P. breviuscula*. They found differences between the *P. bachus* samples from the two countries that were equivalent to differences between *P. barbata* and each of the two *P. bachus* morphs, suggesting species-level differences between all three. These genetic discrepancies were supported by work of Kemp (2010), who observed that there are a number of differences between individuals from Australian and New Zealand waters and that morphometric and meristic characteristics of *Pseudophycis* species in Australian waters have been poorly documented. She compared 50 Australian specimens with 160 from New Zealand, both series identified as *P. bachus,* and found

significant differences in mean values for the second dorsal (50.2 vs. 42.8, respectively) and anal (52.1 vs. 45.0) fin ray counts, as well as pyloric caeca (9.6 vs. 6.0). These observations provided the incentive to further compare the Australian and New Zealand populations with each other and with the other two long-recognised members of the genus, *P. barbata* and *P. breviuscula*. The outcome was a recognition of four easily distinguished species in the genus and the initiation of research on the scientific name for the Australian Red Cod.

The Australian Red Cod is a relatively common demersal species, distributed in the shelf waters of south-eastern Australia (Gomon in Gomon et al., 2008). It is an important prey species for some high trophic level predators, including little penguins, *Eudyptula minor* (Chiaradia et al., 2003; Cullen et al., 1992; Montague and Cullen, 1988), Australian fur seals, *Arctocephalus pusillus doriferus* (Gales and Pemberton, 1994; Hume et al., 2004; Kirkwood et al., 2008; Littnan et al., 2007), and New Zealand fur seals, *Arctocephalus forsteri* (Page et al., 2005). The trophic role of Australian Red Cod as prey, coupled with its relatively common occurrence, suggests that this species is particularly important in Australian waters. Humans include these fishes as part of the non-targeted bycatch consumed annually, although the species is more frequently discarded than retained (pers. comm. M. Tudman, Bycatch Reduction Program Manager, Australian Fisheries Management Authority, 2008).

This contribution provides a name for the endemic Australian Red Cod, a detailed description that distinguishes it from the New Zealand *P. bachus*, descriptions for the four species in the genus and a dichotomous key to the species.

Methods

Morphometric methodology mostly followed Paulin (1983), Trunov (1990), and Markle and Melendez (1988); measurements were taken directly (point-to-point) except that measurements between fins were horizontal distances between vertical projections at the origins of each fin, caudal peduncle length was taken from the posterior end of the anal fin base to the hypural joint, caudal-fin length was from the hypural joint to the fin tip, and lengths of gill rakers and filaments were taken at or adjacent to the angle of the gill arch. In lists of specimens examined, numbers of specimens and their standard lengths in mm are placed in parentheses after registration numbers, except for lots containing only a single specimen where only the length is presented. Meristic methods are those of Hubbs and Lagler (1947) where counts of unpaired fins and vertebrae were taken from radiographs, the number of trunk centra was counted from the cranium to the last centrum with pleural ribs and counts of tail centra exclude the urostyle. Selected meristic and relative morphometric ranges for the four congeners are presented in Tables 2–4. Other materials examined are in the ichthyological collections of the Australian Museum (AMS), Natural History Museum (formerly British Museum [Natural History]; BMNH), Australian National Fish Collection (CSIRO), Museums Victoria (NMV), Museum of New Zealand Te Papa Tongarewa (NMNZ), South Australian Museum (SAMA), Staatliches Museum für Naturkunde, Stuttgart (SMNS) and Western Australian Museum (WAM).

Genetic material and sequences. A genetic analysis of mitochondrial cytochrome oxidase subunit I (COI) gene was carried out on 72 sequences from muscle tissues, representing 5 terminal taxa of the family Moridae.

The dataset included 61 sequences from the BOLD database (www.boldsystems.org) and 11 sequences newly generated for this study (see Appendix 1 for list of material and BOLD and GenBank accession numbers; vouchers for tissues yielding sequences in the material examined lists are indicated by a dagger †), including 18 specimens of *Pseudophycis bachus* from New Zealand, 23 *P. barbata* from Australia and New Zealand, 12 *P. breviuscula* from Australia and New Zealand, 12 *P. palmata* from Australia, and 7 *Auchenoceros punctatus* from New Zealand as a morid outgroup.

Genomic DNA was extracted from the 11 (7 *P. bachus* [including neotype], 2 *P. breviuscula* and 2 *P. barbata*) additional ethanol-preserved muscle tissues (Appendix 1) using DNeasy blood and tissue kit (Qiagen). A fragment of the COI gene was PCR amplified and sequenced using thermocycling conditions and primers (FishF2 and FishR1) from Ward et al., 2005). PCR products were purified by digestion with the ExoProStar (Illustra) or with the Zymo DNA Clean and Concentrator (Zymo Research, USA), following the manufacturer's instructions. PCR products were sequenced in both directions on an ABI-3730 (Massey University Genome Service, Palmerston North, New Zealand or Macrogen, Seoul, South Korea). Newly generated sequences were deposited in GenBank (see Appendix 1 for a list of voucher specimens and their accession numbers).

Phylogenetic analyses. All 72 sequences were individually aligned in ClustalW using the software Geneious Prime v10.0.5. The COI alignment contained no insertions or deletions. Maximum likelihood, neighbour joining and maximum parsimony trees were used to visualise distance relationships within and between species; node support was assessed with 1,000 bootstrap replications of each tree. For the maximum likelihood analyses, the most appropriate model of sequence evolution for each dataset was determined using the Akaike information criterion in ModelTest; the HKY + G model was selected (Hasegawa et al., 1985) because it was the best performing of 24 different nucleotide substitution models tested in the model selection option of MEGA version X (Kumar et al., 2018). A discrete gamma distribution was used to model evolutionary rate differences between sites (5 categories, +G, parameter = 0.3772). In addition, a neighbour joining tree was estimated using p-distances (uncorrected distances). The p-distance is the proportion of nucleotide sites at which two sequences being compared are different. It is obtained by dividing the number of nucleotide differences by the number of nucleotides

compared. It does not make any correction for multiple substitutions at the same site, substitution rate biases (e.g. differences in the transitional and transversional rates), or differences in evolutionary rates between sites. For the maximum parsimony analyses, a heuristic search algorithm with 1000 random addition sequence replicates and tree bisection and reconnection branch swapping methodology was used. Nodal support was tested with 500 bootstrap pseudo-replicates, with ten random addition replicates for each pseudo-replicate.

Multivariate analysis of morphological data

To investigate the *a priori* grouping by species, a canonical analysis of principal coordinates (CAP) was performed using normalised Euclidean distances between specimens (Anderson and Willis, 2003). CAP is equivalent to a classical discriminant analysis. Leave-one-out mis-classification error (Lachenbruch and Mickey, 1967) was used to obtain a direct measure of the ability of the CAP discriminant model to identify species on the basis of the 20 characters. This cross-validation provided a rigorous assessment of the distinctiveness of the four species of *Pseudophycis*. The following 20 characters, measured in 124 *Pseudophycis* specimens of the four species (see material examined), were used in the analysis: anal fin base length, barbel length, caudal peduncle depth, caudal peduncle length, caudal fin length, first dorsal fin base length, first dorsal fin longest ray length, head length, orbit diameter, pectoral fin base width, pectoral fin length, pelvic fin length, postorbital length, pre-dorsal fin length, pre-anal fin length, pre-pectoral fin length, pre-pelvic fin length, pelvic fin origin to anal fin origin length, second dorsal fin base length, and snout length.

Genus *Pseudophycis* Günther, 1862

Pseudophycis Günther, 1862: 350, type species: *Lota breviuscula* Richardson, 1846, by monotypy.

Austrophycis Ogilby, 1897: 90, type species: *Austrophycis megalops* Ogilby, 1897 (= *P. breviuscula*) by monotypy.

Physiculus (*Pseudophycis*) Whitley, 1956: 403, taxonomic decision.

Diagnosis. Morid fishes with an elongate body. Luminescent organs absent. Snout broadly rounded in dorsal view, not projecting greatly beyond mouth, length about equal to interorbital width. Eye diameter much less than postorbital length. Each jaw with broad band of small, depressible, caniniform teeth of uniform size. Vomerine teeth absent. Chin with well-developed, often small, barbel. Branchiostegal rays seven. Gill rakers of outer branchial arch short or of moderate length. Otolith with ostium approximately equal to the cauda (1:1 to 1:1.4), the crista superior as long as or longer than the crista inferior; otolith thickness 20–22% of its length (Paulin, 1983). Scales small, covering body and head; extending onto loose membranes enveloping the bases of dorsal and anal fins; lateral line pores at ends of short tubes from naked strip not associated with individual scales. Two dorsal fins and one anal fin, first dorsal slightly taller than, immediately adjacent to and joined to second by low membrane, with 8–14 rays, first ray not prolonged; second dorsal and anal fins with elongate bases, of nearly uniform height; caudal fin separate, rounded or truncate. Ventral fins composed of five or six rays, the two outermost longest and projecting beyond fin membrane but not greatly prolonged.

Etymology. The feminine name *Pseudophycis* is an amalgamation of the Greek words *pseudos*, meaning "lie" or "false", and *phykis*, "a fish living among seaweeds" (Brown, 1954) and the source word of the scientific name for the North Atlantic gadid genus *Phycis* Walbaum, 1792, in reference to the overall resemblance of species of the two genera to one another.

Distribution. Species of the genus are endemic to coastal waters of temperate Australia and New Zealand.

Remarks. Species referable to the genus *Pseudophycis* were described or treated as members of seven morid genera based on the superficial resemblances of species in the genera to one another. These include: *Gadus* Linnaeus, 1758, type species *Gadus morhua* Linnaeus, 1758, by subsequent designation of Jordan and Gilbert (1883: 802); *Enchelyopus* Bloch and Schneider, 1801, type species *Gadus cimbricus* Bloch and Schneider, 1801, by subsequent designation of Jordan and Evermann (1898: 2560); *Lota* Oken, 1817, type species *Gadus lota* Linnaeus, 1758, by subsequent tautonomy (Fricke et al., 2019); *Lotella* Kaup, 1858, type species *Lota phycis* Temminck and Schlegel, 1846, by monotypy and *Physiculus* Kaup, 1858, type species *Physiculus dalwigki* Kaup, 1858, by monotypy (see species treatments for details). *Austrophycis* Ogilby, 1897, caused particular confusion until Sazanov (2001: 343) identified the type specimen of *A. megalops* as *P. breviuscula* (Richardson, 1846). The genus *Pseudophycis* comprises four species.

Genetic analysis. Concerted efforts to document genetic sequences for the CO1 gene across Australasian fish species as part of the Fish Barcode of Life project provided an additional means of testing suspect species concepts. A preliminary comparison of sequences of New Zealand and Australian specimens identified as *P. bachus* and *P. barbata* in BOLD had already revealed potentially cryptic sister species on either side of the Tasman Sea. Sequences for specimens identified as *P. bachus* had low divergence among specimens within Australia (0.002) and within New Zealand (0.000) but high sequence divergence in the pooled data (0.086) typical of species pairs (Smith et al., 2008: 8, fig. 5).

A comparison of a larger set of sequences for Australian and New Zealand specimens identified as species of *Pseudophycis*, plus sequences of specimens of *Auchenoceros punctatus* as an outgroup, generated a tree with five inferred species branches, four having a common basal node for vouchers identifiable as *P. barbata*, *P. breviuscula*, *P. bachus* and *P. palmata* (Ward pers. comm.; fig. 1). Importantly, the branches of *P. bachus* and *P. palmata,* previously thought to be conspecific, are of about the same lengths as those of *P. barbata* and *P. breviuscula*, despite the morphological differences distinguishing the latter two (Table 1).

Key to species of *Pseudophycis*

1. Caudal margin truncate with angular corners in specimens larger than about 150 mm SL, central caudal fin rays distinctly shorter than those extending to the corners; basal portion of pectoral fin with distinct dark blotch or spot 2

– Caudal margin rounded with rounded corners, central caudal fin rays equal in length or longer than those extending to the corners; no distinct dark blotch or spot basally on pectoral fin 3

2. Dark blotch or spot basally on pectoral fin extending dorsally onto body; second dorsal fin with 40–45 rays; anal fin with 42–48 rays; total vertebrae 44–46 ..... *Pseudophycis bachus*

– Dark blotch or spot basally on pectoral fin not extending dorsally onto body; second dorsal fin with 47–56 rays; anal fin with 50–57 rays; total vertebrae 47–50 ..... *Pseudophycis palmata*

3. Scales above lateral line 16–22; second dorsal fin with 54–59 rays; anal fin with 54–63 rays; pyloric caeca 14–20; total vertebrae 48–51 ..... *Pseudophycis barbata*

– Scales above lateral line 7–9; second dorsal fin with 44–52 rays; anal fin with 49–56 rays; pyloric caeca 6–9; total vertebrae 42–45 ..... *Pseudophycis breviuscula*

***Pseudophycis palmata* (Klunzinger, 1872)**

Proposed name: Australian Red Cod (Australian Standard)

Figures 1, 2, 3A, 4, 5; Tables 1–4

Physiculus palmatus Klunzinger, 1872: 38. Type locality: Hobsons Bay, Victoria, Australia. Types: SMNS 1589.

Pseudophysis barbatus (*nec* Günther, 1862). McCoy, 1878: 29, pl. 20 (in part; description).

Pseudophycis bacchus (*nec* Forster in Bloch and Schneider, 1801). Günther, 1880a: 28 (Twofold Bay, NSW); Waite, 1899: 119 (distribution).

Pseudophycis bachus (*nec* Forster in Bloch and Schneider, 1801). Ogilby, 1886: 48 (list, in part); Edgar et al., 1982: 32, fig. 17 (description, in part); Last et al., 1983: 234, fig. 21.7 (description, in part); Paulin, 1983: 93 (distribution, in part); Hutchins and Swainston, 1986: 34, 124, fig. 113 (description); May and Maxwell, 1986: 194 (description); Paxton and Hanley in Paxton et al., 1989: 302 (list, in part); Grant, 1991: 75, fig. 164 (list, in part); Gomon in Gomon et al., 1994: 333, fig. 297 (description, in part); Yearsley et al., 1999: 87, fig. (description); Paxton et al., 2006: 616 (taxonomy, in part); Gomon in Gomon et al., 2008: 313, fig. (description, in part).

Physiculus bachus (*nec* Forster in Bloch and Schneider, 1801). Waite, 1904: 24; Stead, 1906: 86 (description, in part); Waite, 1907: 18, fig. (South Australia); Stead, 1908: 48, pl. 16; Waite, 1921: 67; McCulloch, 1921: 42; McCulloch, 1922: XVII, 32; Waite, 1923: 92, fig. (description, in part); Lord and Scott, 1924: 8, 43 (description, in part); Lord, 1927: 13; McCulloch, 1927: 32, pl xi, fig. 112a (list); Waite, 1928: 6 (listed); McCulloch, 1929: 129; McCulloch, 1930: 129 (in part, listed); Norman, 1935: 3; Norman, 1937: 54, 55 (in part, listed); Munro, 1961: 62, fig. 441, (description; in part); Scott, 1962: 84, fig. (description, in part); Whitley, 1962: 58; Whitley, 1964: 40 (list, in part); Walker, 1972: 2; Suda, 1973: 2150–2152 (distribution); Scott et al., 1974: 95, 96, fig. (description, in part).

Pseudophycis barbata (*nec* Günther, 1862). Kuiter, 1993: 59, fig. (description, in part).

Diagnosis. First dorsal fin with 10–12 rays, second dorsal fin with 47–56 rays; anal fin with 50–57 rays; total vertebrae 47–50; nostrils located about two-thirds to three-quarters of the way from snout tip to eye; gill rakers of outer arch of moderate length, almost as long near angle as opposing gill filaments; chin barbel short, 6–17% HL; scales above lateral line in oblique series from base of first dorsal fin ray 11–15; oblique rows of scales intersecting with lateral line 96–116; pyloric caeca 8–10; caudal fin truncate with angular corners in specimens larger than about 150 mm SL, middle rays shorter than rays extending to corners; dark blotch basally on pectoral fin not extending onto side above fleshy pectoral fin base. A large species reaching at least 598 mm TL or approximately 532 mm SL (Kemp, 2010: 26).

Description. (Values for non-type specimens when different from type in parentheses; see Tables 2–4 for summary of selected meristic and comparative morphometric values.) First dorsal fin 11 (10–12, rarely 10, first ray usually minute); second dorsal fin 56 (47–56, rarely 47 or 54–55); anal fin 55 (50–57, rarely less than 51); pectoral fin 22 (22–27); pelvic fin 5 (5 or 6, rarely 6); caudal fin 37 (35–41) rays; gill rakers 4 + 10 (3–4 + 9–11 = 12–15); lateral line pores not associated with individual scales; oblique scale rows intersecting with lateral line unknown (96–116), scales in oblique series above lateral line 15 (11–15), scales in oblique series below lateral line unknown (28–40); vertebrae 16 + 34 (15–18 + 31–34) = 50 (47–50); pyloric caeca 10 (8–10).

Table 1. Estimates of evolutionary divergence over sequence pairs within (left) and between (right) species. Kimura-2-parameter genetic distances as averages over all sequence pairs within species are in the left column, with standard error estimates on the right (left table). Genetic distances as averages over all sequence pairs between species are below the diagonal with standard error estimates above it (right table).

Species	Within species			Between species				
				Distance below and Standard Error above diagonal				
	N	Distance	Standard Error	*A. punctatus*	*P. bachus*	*P. breviuscula*	*P. palmata*	*P. barbata*
A. punctatus	7	0.002	0.001		0.017	0.017	0.017	0.017
P. bachus	18	0.005	0.001	0.160		0.015	0.013	0.015
P. breviuscula	12	0.001	0.001	0.170	0.143		0.016	0.011
P. palmata	12	0.005	0.002	0.158	0.092	0.139		0.014
P. barbata	23	0.003	0.001	0.171	0.127	0.085	0.128	

Table 2. Selected counts for types and representative specimens of the four species of *Pseudophycis*.

Meristic character	*P. palmata*				*P. bachus*				*P. barbata*				*P. breviuscula*			
	type	range	mean ± std dev	N	type	range	mean ± std dev	N	type	range	mean ± std dev	N	type	range	mean ± std dev	N
First dorsal fin rays	11	**10 - 12**	11.3 ± 0.5	47	11	**11 - 13**	11.5 ± 0.6	33	10	**10 - 11**	10.2 ± 0.4	36	9	**8 - 10**	9.2 ± 0.6	49
Second dorsal fin rays	56	**47 - 56**	50.7 ± 2.3	47	42	**40 - 45**	42.5 ± 1.1	33	59	**54 - 59**	56.0 ± 1.6	36	46	**44 - 52**	47.6 ± 1.8	48
Anal fin rays	55	**50 - 57**	54.0 ± 1.9	48	45	**42 - 48**	45.2 ± 1.5	33	59	**54 - 63**	57.4 ± 2.1	36	50	**49 - 56**	51.8 ± 2.0	46
Pectoral fin rays	22	**22 - 27**	24.3 ± 1.1	28	24	**22 - 25**	23.8 ± 0.8	38	25	**24 - 27**	25.7 ± 0.7	31	21	**20 - 23**	21.9 ± 0.8	22
Precaudal vertebrae	16	**15 - 18**	16.1 ± 0.5	46	16	**16 - 17**	16.2 ± 0.4	33		**14 - 16**	15.1 ± 0.6	35	13	**11 - 14**	12.2 ± 0.6	48
Caudal vertebrae	34	**31 - 34**	32.8 ± 0.7	46	29	**27 - 30**	28.8 ± 0.7	33		**33 - 37**	34.7 ± 1.0	35	31	**30 - 33**	31.4 ± 0.7	48
Total vertebrae	49	**47 - 50**	48.8 ± 0.7	47	45	**44 - 46**	45.0 ± 0.6	33		**48 - 51**	49.8 ± 0.8	35	44	**42 - 45**	43.6 ± 0.8	48
Lower gill rakers	10	**9 - 11**	9.7 ± 0.6	30	10	**10 - 12**	10.5 ± 0.6	38		**8 - 11**	9.5 ± 0.6	34	8	**7 - 8**	7.7 ± 0.4	23
Upper gill rakers	4	**3 - 4**	3.6 ± 0.5	30	4	**4 - 5**	4.4 ± 0.5	38		**3 - 4**	3.5 ± 0.5	34	3	**2 - 3**	2.7 ± 0.4	23
Total gill rakers	14	**11 - 15**	13.3 ± 0.8	30	14	**14 - 16**	14.9 ± 0.8	38		**12 - 14**	13.0 ± 0.7	34	11	**9 - 12**	10.5 ± 0.8	22
Upper procurrent caudal fin rays	5	**5 - 8**	7.3 ± 0.9	27	8	**6 - 9**	7.2 ± 1.0	23	6	**5 - 7**	5.8 ± 0.8	21		**5 - 7**	5.9 ± 0.7	39
Principal (branched) caudal fin rays	25	**21 - 26**	22.8 ± 1.2	26	20	**19 - 24**	21.3 ± 1.4	23	20	**20 - 22**	21.0 ± 0.9	21		**15 - 21**	18.1 ± 1.3	38
Lower procurrent caudal fin rays	7	**6 - 8**	7.1 ± 0.4	26	8	**6 - 10**	7.9 ± 1.0	23	7	**5 - 7**	6.1 ± 0.8	21		**5 - 7**	5.8 ± 0.7	38
Total caudal fin rays	37	**35 - 41**	37.3 ± 1.3	42	36	**33 - 39**	36.4 ± 1.4	23	33	**32 - 35**	33.0 ± 1.0	18		**26 - 32**	29.7 ± 1.5	37
Transverse scale rows		**96 - 116**	109 ± 7.2	14	112	**102 - 136**	118 ± 8.7	35		**123 - 162**	141 ± 10.5	27	93	**77 - 93**	87.5 ± 4.7	17
Scales above lateral line	15	**11 - 15**	12.9 ± 1.4	27	11	**10 - 12**	11.3 ± 0.8	34		**16 - 22**	18.1 ± 1.6	30	7	**7 - 9**	7.8 ± 0.6	22
Scales below lateral line		**28 - 40**	34.5 ± 3.8	14	30	**26 - 34**	29.5 ± 2.4	26	38	**38 - 56**	49.2 ± 5.0	27	23	**22 - 28**	25.2 ± 1.9	16
Pyloric caeca	10	**8 - 10**	9.5 ± 0.8	8	6	**6**	6.0 ± 0.0	29		**14 - 20**	16.0 ± 1.5	20		**7 - 8**	7.5 ± 0.5	8

Table 3. Frequencies of selected meristic characters in *Pseudophycis* species. Shaded values are those of types.

Second dorsal fin rays	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	N
P. palmata								2	8	4	10	6	7	4	3	2	**1**				**47**
P. bachus		1	4	**13**	10	4	1														**33**
P. barbata															7	9	7	5	5	**3**	**36**
P. breviuscula					1	2	**11**	13	5	11	1	2	2								**48**

Anal fin rays	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	N
P. palmata									1	5	4	11	7	**10**	3	7							**48**
P. bachus	1	4	5	**8**	8	6	1																**33**
P. barbata													2	4	7	8	6	**5**	1	1	1	1	**36**
P. breviuscula								7	**8**	5	8	8	5	4	1								**46**

Total caudal fin rays	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	N
P. palmata										3	10	**6**	19	2	1	1	**42**
P. bachus								1	1	3	**6**	9	1	2			**23**
P. barbata							7	**5**	5	1							**18**
P. breviuscula	**1**	2	4	7	12	7	4										**37**

Caudal vertebrae	27	28	29	30	31	32	33	34	35	36	37	N
P. palmata					1	13	26	**6**				**46**
P. bachus	1	9	18	5								**33**
P. barbata							4	11	12	**7**	1	**35**
P. breviuscula				4	**23**	18	3					**48**

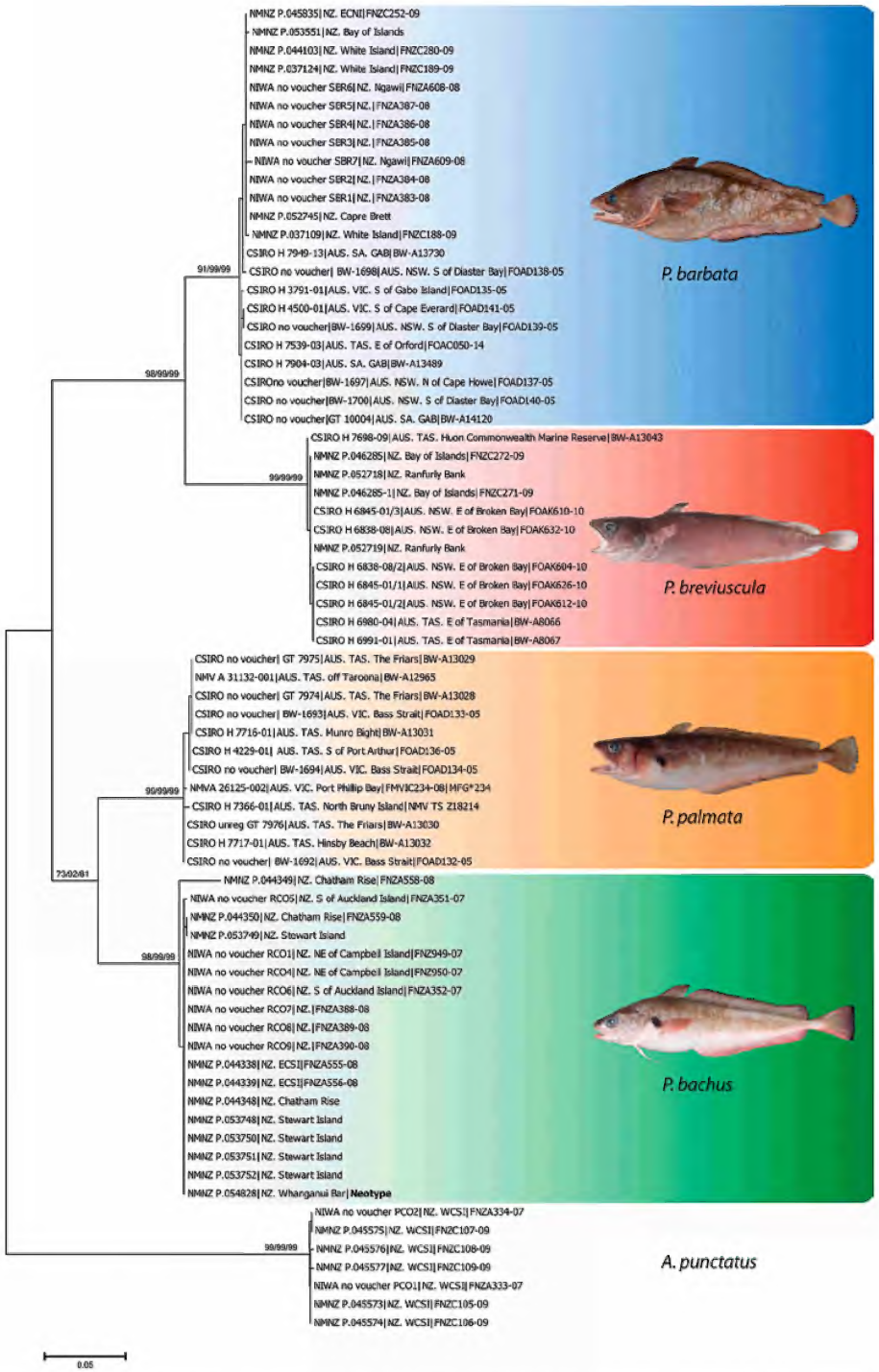
Total vertebrae	42	43	44	45	46	47	48	49	50	51	N
P. palmata						2	10	29	**6**		**47**
P. bachus			6	**20**	7						**33**
P. barbata							2	8	19	6	**35**
P. breviuscula	3	18	**21**	6							**48**

Scales above lateral line	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	N
P. palmata					4	10	**4**	4	5								**27**
P. bachus				6	**12**	16											**34**
P. barbata										4	8	10	2	3	1	2	**30**
P. breviuscula	7	13	2														**22**

Pyloric caeca	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	N
P. palmata			1	2	**6**											**8**
P. bachus	**29**															**29**
P. barbata									2	7	5	3	2		1	**20**
P. breviuscula		4	4													**8**

Table 4. Selected proportional measurements for types and representative specimens of the four species of *Pseudophycis*.

Measurement	*P. palmata* type	*P. palmata* range	*P. palmata* mean ± std dev	*P. palmata* N	*P. bachus* type	*P. bachus* range	*P. bachus* mean ± std dev	*P. bachus* N	*P. barbata* type	*P. barbata* range	*P. barbata* mean ± std dev	*P. barbata* N	*P. breviuscula* type	*P. breviuscula* range	*P. breviuscula* mean ± std dev	*P. breviuscula* N
Standard Length (mm)	172	**73.5 - 380**			351	**110 - 539**			394	**82.0 - 531**			152	**59.4 - 179**		
% SL																
Body depth (anal fin origin)	23.6	**18.7 - 26.5**	22.0 ± 1.8	31	19.5	**18.4 - 23.7**	20.9 ± 1.4	36		**19.7 - 29.3**	24.1 ± 2.0	34	22.8	**20.6 - 23.3**	21.8 ± 0.8	28
Caudal peduncle depth	5.5	**4.1 - 5.9**	5.0 ± 0.4	32	3.8	**3.8 - 5.9**	4.5 ± 0.4	38	3.8	**3.3 - 5.2**	4.5 ± 1.0	35	4.0	**3.9 - 4.8**	4.3 ± 0.3	29
Caudal peduncle length	8.9	**6.7 - 10.8**	9.1 ± 0.9	31	8.5	**7.7 - 10.5**	9.1 ± 0.7	38	5.4	**5.2 - 9.2**	6.9 ± 1.0	35	4.8	**5.7 - 8.5**	7.2 ± 0.8	29
Head length	26.1	**25.9 - 30.0**	27.8 ± 0.9	33	26.5	**25.9 - 29.6**	27.1 ± 0.8	38	23.3	**23.3 - 31.6**	28.8 ± 1.6	35	25.8	**23.4 - 26.0**	24.8 ± 0.6	29
Head depth (eye)	12.8	**10.2 - 18.4**	13.9 ± 2.0	30	11.7	**10.2 - 15.6**	11.8 ± 1.1	37		**11.0 - 17.9**	13.6 ± 1.4	33	12.1	**10.8 - 15.2**	12.8 ± 1.1	27
Orbital diameter	7.3	**5.3 - 9.7**	7.4 ± 0.9	33	5.6	**4.6 - 8.1**	6.2 ± 0.9	38	4.9	**4.9 - 8.3**	6.9 ± 0.9	35	7.1	**6.2 - 8.7**	7.2 ± 0.8	29
Postorbital length	13.1	**12.2 - 16.0**	14.0 ± 0.9	33	14.1	**12.4 - 16.4**	14.2 ± 0.8	38	12.2	**7.5 - 17.7**	14.9 ± 1.9	35	14.7	**11.4 - 14.3**	13.3 ± 0.8	29
Interorbital width	8.7	**7.9 - 10.0**	9.0 ± 0.6	32	8.8	**7.2 - 9.9**	8.6 ± 0.6	38		**6.5 - 8.8**	8.0 ± 0.5	34	6.4	**5.5 - 7.4**	6.3 ± 0.4	29
Suborbital depth	2.7	**1.4 - 3.2**	2.2 ± 0.4	32	2.5	**1.5 - 3.3**	2.5 ± 0.3	38		**1.7 - 3.7**	2.6 ± 0.6	34	2.1	**1.3 - 2.4**	2.0 ± 0.3	29
Snout length	7.6	**6.7 - 9.1**	7.8 ± 0.6	33	7.5	**7.1 - 9.0**	8.0 ± 0.5	38	7.5	**6.5 - 9.6**	8.1 ± 0.7	35	5.9	**5.1 - 7.0**	6.2 ± 0.5	29
Upper jaw length	15.0	**13.6 - 16.2**	15.2 ± 0.6	33	13.9	**12.8 - 14.8**	13.9 ± 0.4	38	12.3	**12.3 - 17.5**	15.6 ± 1.1	35	13.4	**11.0 - 13.2**	12.5 ± 0.5	29
Barbel length	3.0	**1.7 - 4.9**	3.5 ± 0.8	32	3.2	**2.4 - 4.8**	3.4 ± 0.6	36	4.9	**4.7 - 9.6**	6.6 ± 1.1	34	5.4	**4.9 - 7.5**	6.3 ± 0.7	28
Pre-dorsal fin length	31.2	**28.1 - 32.7**	30.6 ± 1.1	32	28.2	**27.5 - 31.8**	29.5 ± 1.1	38	34.4	**29.2 - 37.4**	32.8 ± 1.7	35	31.0	**27.8 - 31.6**	30.0 ± 1.0	29
Pre-anal fin length	41.5	**37.9 - 48.0**	43.6 ± 2.5	31	42.4	**39.6 - 47.3**	43.9 ± 1.7	37	45	**38.6 - 51.0**	44.8 ± 3.5	35	44.1	**35.0 - 41.4**	38.0 ± 1.9	27
Pre-pectoral fin length	27.5	**26.3 - 32.6**	28.7 ± 1.3	32	26.8	**25.8 - 30.2**	27.9 ± 1.0	38	25.7	**25.7 - 32.7**	29.5 ± 1.5	35	27.1	**24.5 - 28.5**	26.0 ± 1.0	29
Pre-pelvic fin length	18.2	**18.2 - 26.0**	20.5 ± 2.0	31	19.6	**17.0 - 22.2**	19.8 ± 1.2	38	18.1	**16.4 - 23.6**	19.3 ± 1.9	35	15.1	**13.9 - 21.1**	17.2 ± 1.9	27
Pelvic fin origin to anal fin origin	24.4	**18.5 - 30.5**	24.6 ± 2.4	30	24.2	**22.8 - 28.7**	25.4 ± 1.6	37	27.9	**20.2 - 33.5**	26.8 ± 3.3	35	30.4	**18.0 - 25.5**	22.1 ± 2.1	27
First dorsal fin base length	10.2	**6.8 - 12.1**	10.4 ± 1.2	32	10.4	**9.2 - 13.1**	11.0 ± 0.9	37	8.3	**6.8 - 13.6**	9.2 ± 1.2	35	9.9	**7.9 - 19.1**	10.6 ± 2.7	29
First dorsal fin longest ray	17.3	**8.5 - 17.3**	12.6 ± 1.9	31	10.7	**9.8 - 15.0**	11.9 ± 1.2	35	7.6	**7.6 - 15.0**	10.0 ± 1.4	35	9.0	**8.6 - 12.8**	11.2 ± 1.0	18
Second dorsal fin base length	54.5	**47.9 - 56.7**	52.9 ± 2.0	33	53.7	**48.6 - 56.2**	53.1 ± 1.7	38	53.2	**50.4 - 62.3**	54.8 ± 2.7	35	55.9	**53.0 - 60.2**	56.7 ± 1.8	29
Anal fin base length	50.9	**45.0 - 57.4**	51.1 ± 2.6	33	50.2	**45.4 - 53.8**	50.1 ± 1.7	37	51.9	**46.3 - 58.4**	53.0 ± 2.5	35	56.5	**53.8 - 66.0**	58.3 ± 2.8	29
Pectoral fin length	16.6	**13.5 - 17.7**	15.8 ± 1.0	33	17.2	**14.6 - 19.4**	17.1 ± 1.3	38	11.2	**11.2 - 17.5**	15.8 ± 1.3	35	16.7	**13.6 - 17.5**	15.7 ± 1.0	29
Pelvic fin length	15.1	**11.7 - 17.3**	14.3 ± 1.5	31	16.0	**11.5 - 21.1**	16.7 ± 2.0	36	13.3	**13.3 - 24.9**	20.2 ± 2.5	35	17.6	**16.6 - 21.6**	19.1 ± 1.2	27
Caudal fin length	10.3	**9.9 - 15.3**	12.2 ± 1.4	32	13.3	**11.2 - 15.6**	13.7 ± 1.2	37	8.6	**8.6 - 15.3**	12.7 ± 1.5	35	12.7	**11.4 - 18.1**	13.6 ± 2.0	28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CSIRO H 4500-01|AUS. VIC. S of Cape Everard|FOAD141-05
CSIRO no voucher|BW-1699|AUS. NSW. S of Diaster Bay|FOAD139-05
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CSIRO H 7904-03|AUS. SA. GAB|BW-A13489
CSIROno voucher|BW-1697|AUS. NSW. N of Cape Howe|FOAD137-05
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P. barbata
91/99/99
98/99/99
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CSIRO H 6980-04|AUS. TAS. E of Tasmania|BW-A8066
CSIRO H 6991-01|AUS. TAS. E of Tasmania|BW-A8067
P. breviuscula
99/99/99
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CSIRO H 7366-01|AUS. TAS. North Bruny Island|NMV TS Z18214
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CSIRO H 7717-01|AUS. TAS. Hinsby Beach|BW-A13032
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P. palmata
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98/99/99
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99/99/99
A. punctatus
0.05

Figure 1. Hasegawa-Kishino-Yano maximum likelihood tree of 65 COI sequences from four purported species of *Pseudophycis*, along with seven sequences for an outgroup species, *Auchenoceros punctatus*. Percentage bootstrap values followed by bootstrap values in p-distance neighbour joining and maximum parsimony trees are given for all well supported nodes (2 of 3 exceeding 80%). Specimen numbers are those of registered museum vouchers or sequence numbers in the Barcode of Life Database (BOLD, http://www.barcodinglife.org/).

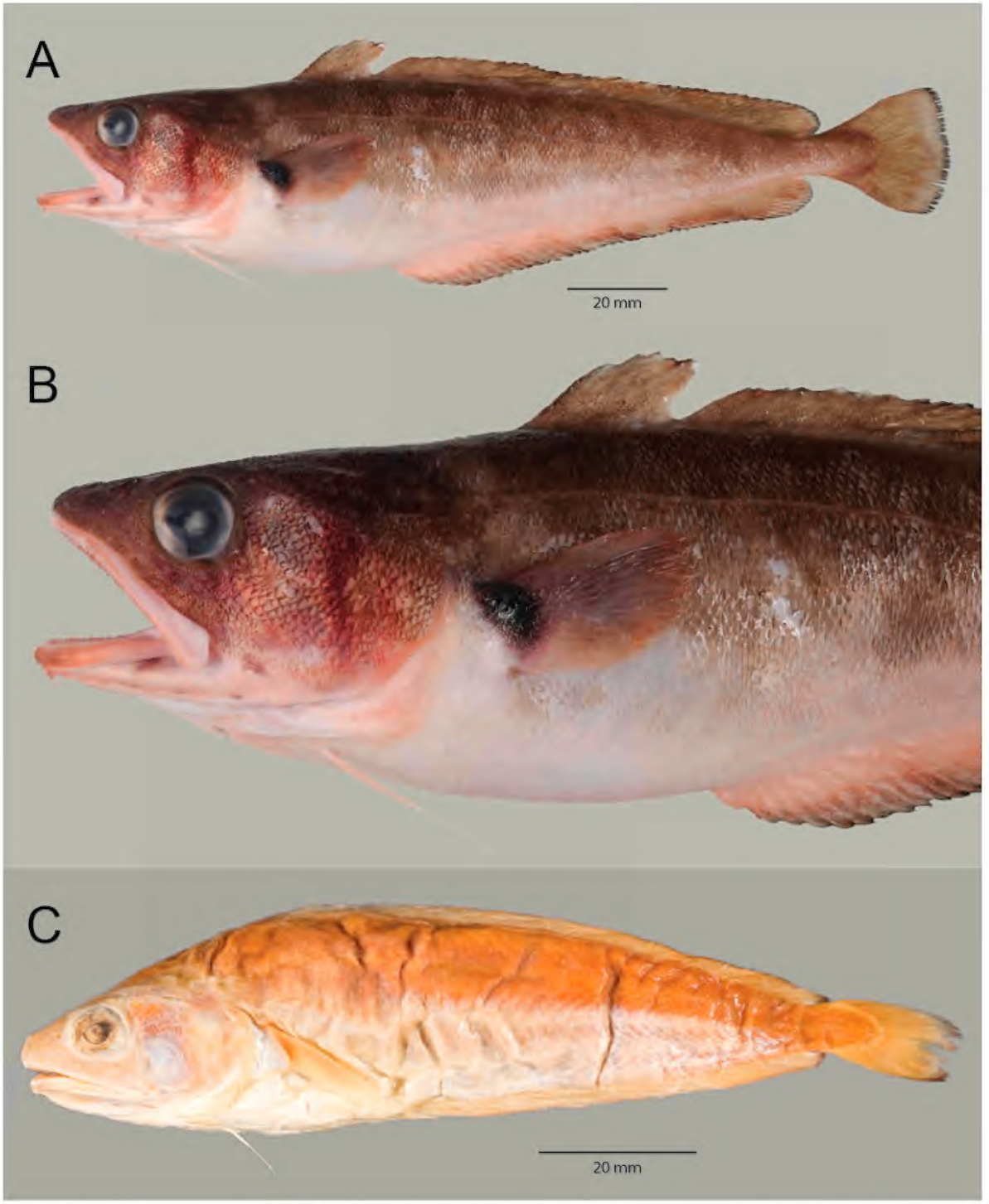

Figure 2. *Pseudophycis palmata*. A, B, CSIRO H 7366-01, 265 mm SL, Storm Bay, east of Variety Bay on North Bruny Island, Tasmania, Australia, fresh specimen, lateral view of body and lateral view of head and anterior body with black pectoral blotch, respectively, (photographs C. Devine, CSIRO); C, SMNS 1589, holotype, 172 mm SL, Port Phillip, Hobsons Bay, Victoria, Australia (photograph C. Struthers, NMNZ).

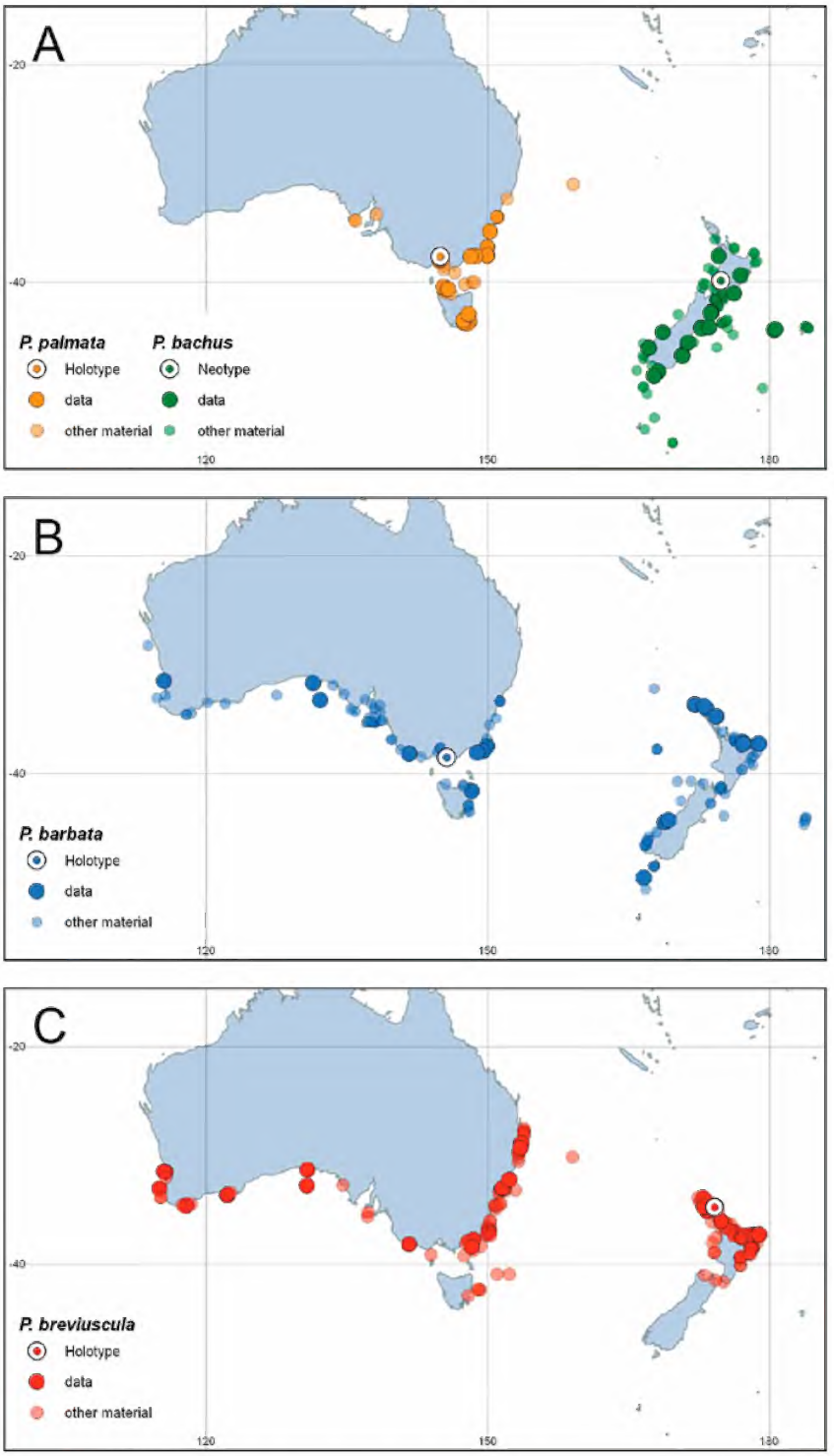

Figure 3. Collection localities for specimens of *Pseudophycis* spp. in museums. A, *P. bachus*, green and *P. palmata*, orange; B, *P. barbata*, blue; C, *P. breviuscula*, red.

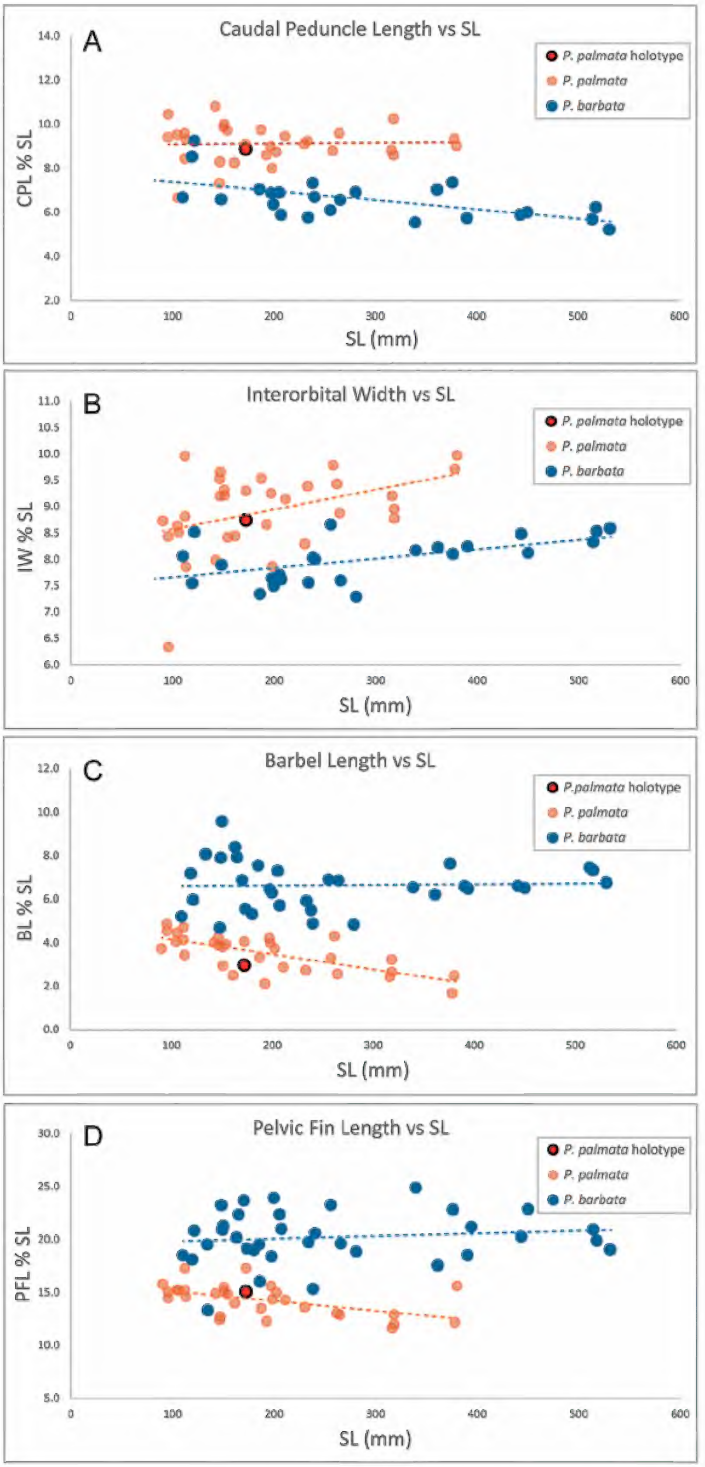

Figure 4. Plots of proportional measurements (% SL) against standard lengths for non-type specimens of *Pseudophycis palmata*, *P. barbata* and holotype of *P. palmata*. A, caudal peduncle length; B, interorbital width; C, barbel length; D, pelvic fin length.

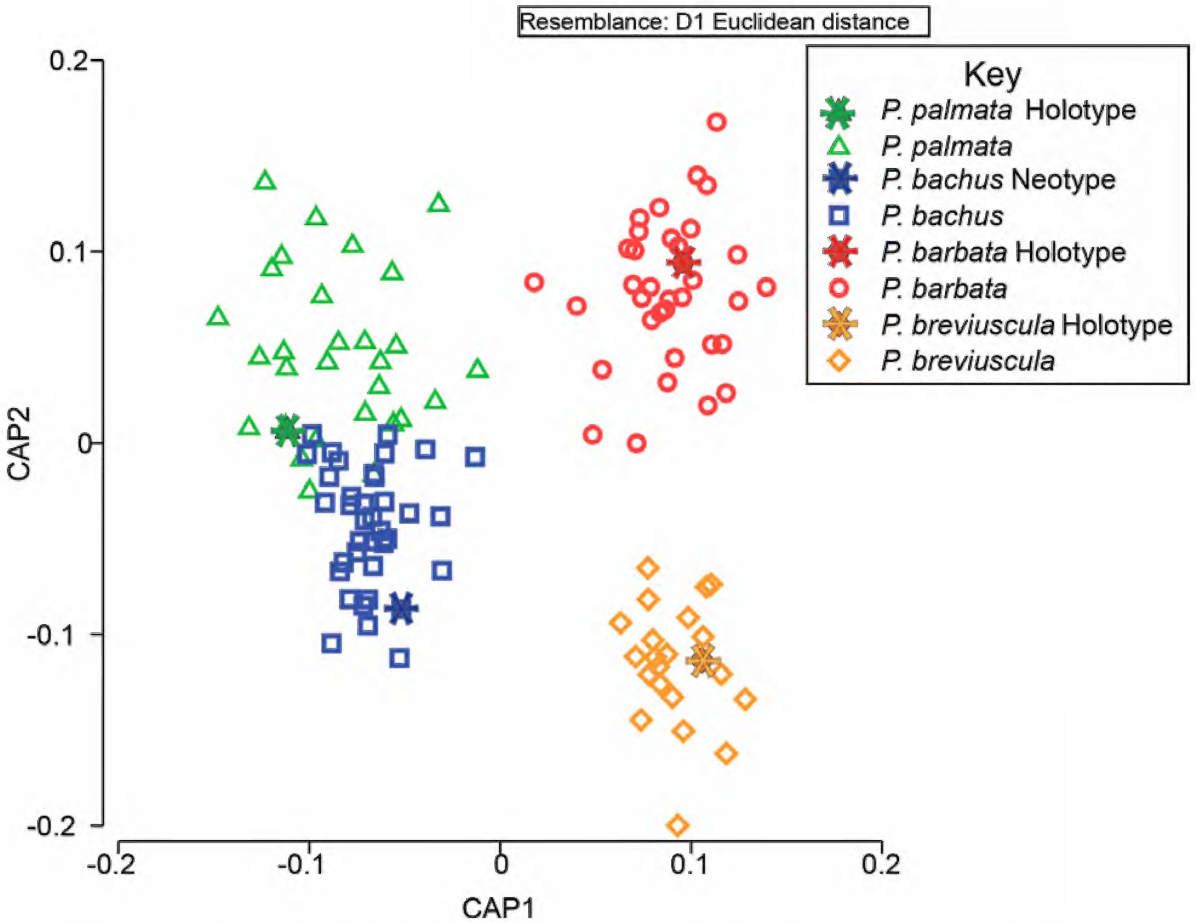

Figure 5. Scatter plot of canonical analysis of principal coordinates scores on the first and second canonical axes for 124 specimens of *Pseudophycis*, including types.

Body moderately slender, compressed laterally (fig. 2), greatest depth at anal fin origin 23.6 (18.7–26.5)% SL, tapering uniformly from second dorsal fin origin to shallow caudal peduncle; caudal peduncle moderately short, 8.9 (6.7–10.8)% SL, strongly compressed, depth subequal to orbital diameter. Distance between middle of anus and base of anal fin slightly less than half suborbital depth. Body cavity extending to above origin of anal fin.

Head acute, of moderate size, length 26.1 (25.9–30.0)% SL, width 14.5 (15.3–21.6)% SL and depth 12.8 (10.2–18.4)% SL; snout of moderate length 7.6 (6.7–9.1)% SL, not projecting in advance of upper jaw, rounded in dorsal view. Nostrils small, located about two-thirds to three-quarters of the way from snout tip to eye, distance from nostril to orbital margin less than (equal to or less than) diameter of combined nostrils; nostrils positioned above horizontal through centre of eye; posterior opening larger than (about half size to larger than) anterior opening, separated from it by raised skin flap; most of margin (most or just posterior opening) encircled by tubular flap. Interorbital broad, slightly convex. Eye of moderate size, orbital diameter 28.0 (18.9–31.5)% HL, 1.33 (0.66–1.87) times in interorbital space, 2.41 (1.65–7.06) times suborbital distance, circular, upper edge of eye adjacent to dorsal margin of head in lateral view, transparent skin covering eye faintly pigmented near orbital dorsal margin. Postorbital moderately long, 0.91 (0.85–1.01) times length of upper jaw. Mouth large, terminal, upper jaw terminating posterior to (at or posterior to) vertical through posterior margin of eye. Jaw teeth caniniform, slightly curved, depressible, band of up to four or five irregular rows in upper jaw with distinct hiatus at symphysis; teeth in outer row more regularly arranged than in inner rows; band tapering near rear of jaw. Teeth of lower jaw similar in form to those of upper jaw; band of two or three rows with broader patch on either side of symphysis, tapering to single, widely spaced row posteriorly; rows almost contiguous across symphysis. Vomerine teeth absent.

Opercular bones strong; upper extremity of gill opening at horizontal through middle of eye; gill membranes continuous across isthmus. Gill rakers on outer arch slender, of moderate length, about 0.8 to 1.3 times length of opposing gill filaments, 8.4–12.2 times in head, their inner margin denticulate. Chin barbel short, subconical 11.3 (6.0–17.4)% HL.

Small cycloid scales covering all of head, including gular region and isthmus, and body except for branchiostegal membranes, surface of maxilla and premaxilla, lower lip and distal parts of fins; thick mucus covering obscuring scales and pores in freshly preserved material. Most head pores tiny, following main cephalic sensory canals; row of slightly raised pores from nostrils to tip of snout and then posteriorly just above lower edge of suborbital; row of enlarged mandibular pores on underside of lower jaw. Lateral line comprising widely spaced pores on short tubes arising from narrow scaleless gap, anterior end curved upwards slightly, then gradually descending to lateral midline below posterior 25% of second dorsal fin, remaining on lateral midline posteriorly.

Membranes of first and second dorsal fins continuous at base; first dorsal originating distinctly behind vertical through pectoral fin base; anterior two-thirds of second dorsal of uniform height, 10th to 12th ray from posterior end of fin longest, its height about 1.4 times length of 2nd ray at anterior end of fin, last ten or so rays progressively shorter; rays of both dorsal fins mostly unbranched, only last 13 to 16 rays, apart from last one to three, branched. Fleshy, fine scale-covered basal sheath on third or more of first dorsal and anterior portion of second dorsal fins; fin rays interconnected by membranes to tips, sheath gradually decreasing slightly in coverage and thickness posteriorly, encompassing about half of second dorsal fin near its insertion; sheath extending onto body for anterior third of combined dorsal fin base, broadest anteriorly, narrower posteriorly. Profile of anal fin like second dorsal fin with comparable unbranched and branched rays. Anal fin enclosed in broad fleshy sheath like dorsal fins; sheath also extending onto body for anterior third or less of fin. Caudal fin truncate with distinct dorsoposterior and ventroposterior corners in adults, posterior margin with slight convex curve; longest rays to corners, middle rays about 85–90% length of longest rays; fin more rounded in juveniles; base of fin covered by indistinct sheath sharply demarcated from scales of caudal peduncle. Pectoral fin tip reaching (not quite to or to) vertical through anal fin origin, sixth or seventh ray longest. Pelvic fin inserted anterior to vertical through posterior edge of preopercle (more posteriorly in some specimens); outer two rays longer than inner rays; second ray longest, 15.1 (11.7–17.3)% SL, nearly twice length of subsequent ray, reaching vertical through first dorsal fin origin.

Fresh colour. (Based on images of non-type material; fig. 2A, B.) Medium brown above extending ventrally to about ventral portion of pectoral fin base, white below, suffused with pinkish hue, especially above anal fin base; lateral line slightly paler at least anteriorly. Underside of head, jaws and barbel white, sometimes tinged with pink. Dorsal, caudal and distal half of anal fins medium brown; proximal half of anal fin white, especially anteriorly, with pink hue; dorsal and anal fins with fine black edge; posterior edge of caudal fin with broad black margin. Pectoral fin medium brown with semi-circular black basal spot covering dorsal 80% of proximal edge of fin, extending little if at all onto side dorsal to fin base. Pelvic fin rays white with pink hue.

Preserved colour. Mostly pale (upper half of head and body pale dusky to dusky, lower half very pale, frequently pearly white. Dorsal, caudal and distal half of anal fins pale dusky; distal edges of dorsal and anal fins with fine dark margin; posterior edge of caudal fin broadly dark; pelvic fin, pectoral fin and basal half of anal fin very pale; pectoral fin with prominent dark spot (faded in type) covering dorsal half or more of basal edge, not extending onto side of body dorsally.

Etymology. The specific epithet *palmata* appears to be Latin for "embroidered with palm branches", although the reason for the name is unknown.

Distribution. Endemic to coastal temperate waters of south-east Australia at least from Port Lincoln, Spencer Gulf, South Australia (34° 44' S, 135° 52' E, SAMA F2766), to Port Stephens, New South Wales (32° 49' S, 152° 05' E, AMS I.25865-003), including all of Tasmania (fig. 3a). An unverified record at Coles Point, South Australia, 34° 22' 06" S, 135° 21' 09" E (SAMA F11864), may extend the distribution slightly farther to the west (fig. 3A). Occurs on soft bottom habitat at 2–115 m.

Remarks. Pseudophycis palmata is closely related to the New Zealand *P. bachus*, with which it was confused (Günther, 1880a: 28; McCulloch, 1921: 42; Ogilby, 1886: 48; Waite, 1904: 24). Both differ from the remaining two congeners by the possession of a black spot or blotch at the base of the pectoral fin and a truncated caudal fin margin in adults. The two also differ from the others in having the lower half of the body and the basal half or more of the anal fin mostly white, rather than tan to brown, although these areas are occasionally suffused with orange to pink in specimens of all four species. Morphometrically, the pair appear to have a deeper caudal peduncle (3.8–5.9, mean 4.7% SL vs. 3.3–5.2, mean 4.4% SL), shorter barbel (1.7–4.9, mean 3.5% SL vs. 4.7–9.6, mean 6.5% SL) and shorter or longer head (25.9–30.0, mean 27.4% SL vs. 23.3–31.6, mean 28.8 in *P. barbata* and 23.4–26.0, mean 24.8% SL in *P. breviuscula*), as well as other relative lengths of features that correspond with the general body form. All four species in the genus are separable by vertical fin ray, scale and vertebral counts, as identified in the above key and in Table 2. Both *P. palmata* and *P. bachus* attain a large size, as does *Pseudophycis barbata* (well over 600 mm SL), while *P. breviuscula* is the smallest species, reaching only about 150 mm SL.

The two *P. bachus*-like species are very similar to each other proportionally, although the eye of the Australian species is slightly larger than that of *P. bachus*, the orbital diameter 5.3–9.7, mean 7.4% SL vs. 4.6–8.1, mean 6.2% SL, the paired fins proportionally shorter, pectoral fin 13.5–17.7, mean 15.8% SL vs. 14.6–19.4, mean 17.1% SL and pelvic fin 11.7–17.3, mean 14.3% SL vs. 11.5–21.1, mean 16.7% SL, and caudal fin similarly shorter 9.9–15.3, mean 12.2% SL vs. 11.2–15.6, 13.7% SL. *Pseudophycis palmata* is readily

separable from *P. bachus* by the smaller pectoral fin blotch that fails to extend onto the body above the pectoral fin base. It also differs subtly from *P. bachus* in having the distal half of the anal fin brownish with a fine black margin rather than whitish, like the basal half, and the black margin confined to the posterior lobe of the fin, if it is present at all. The Australian cognate has fewer transverse scale rows (96–116 vs. 102–136 in *P. bachus*) but more pyloric caeca (8 – 10 vs. 6), anal fin rays (50–57 vs. 42–48) and second dorsal fin rays (47–56 vs. 40–45).

In the course of exploring the taxonomic identity of the Australian Red Cod, the species to which the name *Physiculus palmata* Klunzinger, 1872, is referable became less and less clear. The name was regarded as a junior synonym of *P. barbata* for more than 80 years (McCulloch, 1929: 129). Klunzinger's (1872) original description is inadequate for separating the three species of *Pseudophycis* occurring at or in the vicinity of the type locality. A specimen (SMNS 1589) in the Stuttgart Museum, the repository of Klunzinger's type material, registered the year the name was published, apparently collected at the type locality and clearly identified by Klunzinger as that species, was regarded as a syntype by Fricke (1992: 13; 2005: 48). It is much smaller (173 mm SL) than the 50 cm length given in the description, implying Klunzinger was aware of or had other material. The dark spot on the base of the pectoral fin that is diagnostic for the species, as well as dark pigment on the distal edge of the caudal fin, has completely faded. The only other specimen of *Pseudophycis* (SMNS 2242) dating from that approximate time currently in the Stuttgart collection was identified by Klunzinger in 1877 and is unlikely to have been available when the description was published. We therefore follow Fricke in regarding SMNS 1589 as the only known type.

Although the three species occurring near the type locality are clearly separable by morphological characters, the colours and markings on the type specimen that would have been diagnostic have faded. Meristic characters including vertebral numbers, fin ray and scale counts have ranges that overlap slightly in the two most likely candidate species, *P. barbata* and the Australian *P. bachus* cognate. Unfortunately, the type specimen of *P. palmata* has meristic values that fall in the overlap zone for all but three characters, the number of scales above the lateral line 15 (11–15 in *P. bachus*-like vs. 16–22 in *P. barbata*), total caudal fin rays 37 (35–41 in *P. bachus*-like vs. 32–35 in *P. barbata*) and pyloric caeca 10 (8–10 in *P. bachus*-like vs. 14–20 in *P. barbata*) that favour its identity as the *P. bachus* cognate (Table 1). A comparison of relative morphometric values for the type with those of these two species, however, revealed clear support for the identity of the type as the *P. bachus*-like species with eight of the type's relative measurements (head length, caudal peduncle length, caudal peduncle depth, post-orbital length, interorbital width, barbel length, pelvic fin length and caudal fin length) positioned closer to the *P. bachus*-like species proportional curves relative to standard length (e.g. fig. 4) and curves for the same measurements (not head length) equally close to the proportional curve relative to its head length. Only predorsal fin length has clearly different proportional curves for the *P. bachus*-like species and *P. barbata*, with the predorsal value for the type of *P. palmata* falling equidistant between the curves of the two species for that measurement.

The diagnostics of a CAP analysis revealed that 96.8% of 124 specimens of *Pseudophycis* were correctly classified as their respective species based on the 20 characters examined. By species, the percentage of individuals correctly classified by the CAP discriminant model was 96.6% for *P. palmata* (with one misclassified as *P. bachus*), 97.3% for *P. bachus* (with one misclassified as *P. palmata*), 94.3% for *P. barbata* (with one misclassified as *P. palmata*) and 100% for *P. breviuscula*. Separation of the four species of *Pseudophycis* is shown in fig. 5, with some overlap of *P. palmata* and *P. bachus*. SMNS 1589 (holotype of *P. palmata*) is grouped within the other specimens of *P. palmata* and is well separated from *P. barbata*. Consequently, the CAP analysis and fig. 5 support the taxonomic decision to resurrect *Pseudophycis palmata* as the appropriate name for the Australian endemic previously thought to be conspecific with *P. bachus*. Overlap of *P. palmata* and *P. bachus* is consistent with the historical confusion involving the two species.

Despite its close relationship with *P. bachus*, the first known detailed description of this species appears to be that of McCoy (1878) who based his description of *P. "barbatus"* almost entirely on specimens of the Australian *P. bachus*-like species. That species was probably the common representative of the genus in the Melbourne markets at the time. Meristic and morphometric data presented by McCoy appear to be entirely attributable to specimens of *P. palmata*, with only the illustration (McCoy, 1878: pl. 20) based on a specimen of *P. barbata*. Although several of McCoy's specimens were either lost or obscured by early collection practices, NMV A23366-001 is likely to be the specimen featured in the illustration, while counts and measurements were probably taken from NMV 43104, 43105, A841 and A23366-002. Other old NMV collection specimens of the new species that lack documented provenance probably comprised the remaining three. Considering the frequent occurrence of this species at the type locality of *P. palmata*, together with the strong morphological support discussed above, we consider the name to be applicable to the Australian *P. bachus*-like cognate. Paulin (1983) failed to deal with the name in the synonymies of the three species he recognised.

This species has the most restricted range of Australian *Pseudophycis* species, with no records of it west of Spencer Gulf, South Australia. Its latitudinal limits approach those of *P. bachus* in New Zealand, as do those of the two species occurring in both Australia and New Zealand where bathymetrically feasible.

Material examined. Type. Physiculus palmatus SMNS 1589 (172, holotype) Port Phillip, Hobsons Bay (northernmost section of Port Phillip Bay immediately south of Melbourne), Victoria.

Other material. (51 non-type specimens examined for meristic or morphometric values, 90.1–380 mm SL; see Appendix 2 for additional material in Australasian collections.) **Australia,** ***New South Wales:*** AMS I.34462-004 (2, 230–233) north-east of Lookout Point, Twofold Bay, 37° 4.2' S, 149° 56.1' E, 100 m, J.K. Lowry and S.J. Keable, 26–27 November 1988; AMS I.34567-001 (146) middle of Long Beach,

Batemans Bay, 35° 42' S, 150° 13' E, 50 m, J.K. Lowry and S.J. Keable, 23–24 November 1988; AMS I.34569-003 (112) east of Lookout Point, Twofold Bay, 37° 46' S, 149° 56' E, 50 m, J.K. Lowry and S.J. Keable, 26–27 November 1988; AMS I.34570-001 (3, 117–190) east of Lookout Point, Twofold Bay, 37° 46' S, 149° 55' E, 50 m, 26–27 November 1988. ***Victoria:*** NMV A840-001 (2, 95.5–211) old collection, no data; NMV A840-002 (2, 198–202) old collection, no data; NMV A3859 (187) eastern Bass Strait, 6 km west-south-west of Cape Conran, 37° 49.8' S, 148° 40' E, 26 m, BSS 208 T, M.F. Gomon and R.S. Wilson, 30 July 1983; NMV A8870-001 (4, 95.7–113) and NMV A8870-002 (121) Bass Strait, 1 km off Lake Tyers, 37° 51.1' S, 148° 9' E, 15 m, Marine Science Laboratories, 5 June 1984. ***Tasmania:*** AMS I.23880-004 (192) north of George Town, 40 57.90' S, 146 46.20' E, 50 m, K. Graham and FRV Kapala, 13 July 1980; AMS I.34952-003 (258) mouth of Fortescue Bay, 43° 7.77' S, 147° 59.47' E, 50 m, J.K. Lowry and K. Dempsey, trawl, 9–10 April 1994; CSIRO H 4229-01† (380) south of Port Arthur, 43° 17.3' S, 147° 47.1' E–43° 16.5' S, 147° 49.6' E, 115–119 m, B. Evans, 27 May 1996; CSIRO H 6205-02 (136) Battery Point, CSIRO wharf, 42° 53' S, 147° 20' E, H. Motomura, 20 February 2005; CSIRO H 7366-01† (265) Storm Bay, east of Variety Bay on North Bruny Island, 43° 12.17' S, 147° 27.46' E, 40–45 m, hook and line, A. Pender, 6 May 2012; CSIRO H 7716-01† (350) Munro Bight, 43° 11' S, 147° 59' E, 22 m, A. Pender , January 2012; CSIRO H 7717-01† (362) Hinsby Beach, Taroona, 42° 57.22' S, 147° 20.82' E, 2 m, A. Pender, February 2012; CSIRO T 1186-02† (8, 110-262) Nutgrove Beach, Sandy Bay, Derwent River, P.R. Last, 19 May 1980; CSIRO T 1417 (113 mm SL) Derwent Estuary, 7 m, P.R. Last; NMNZ P.024340 (4: 142–197) Nakyrare Beach, Derwent Estuary, 43° 3.000' S, 147° 22.000' E, FV Ophelia, 29 March 1988; NMV A 1218-001 (316), NMV A 1218-002 (318) central Bass Strait, 20 km north-north-east of North Point, 40° 31.8' S, 145° 22.8' E, 44 m, BSS 116 T, M.F. Gomon, G.C.B. Poore and P. Forsyth, 4 November 1980; NMV A1275 (378) central Bass Strait, 23 km east of Cape Rochon, Three Hummock Island, 40° 22.8' S, 145° 16.998' E, 40 m, BSS 112 T, M.F. Gomon, G.C.B. Poore and P. Forsyth, 3 November 1980; NMV A1528-001 (6, 73.5–161) and NMV A1528-002 (3, 93.6–151) central Bass Strait, 30 km north of Wynyard, 40° 33.07' S, 145° 44.69' E, 67.7 m, 4 February 1981; NMV A 31132-001† (318) off Taroona between Taroona and Alum Cliffs, 42° 57.470' S, 147° 20.797' E, 6 m, hook and line, B. Barlow, 10 May 2014.

Pseudophycis bachus (Forster in Bloch and Schneider, 1801)

Common name: New Zealand Red Cod (new Australian name); red cod, hoka (New Zealand)

Figures 1, 3A, 5, 6; Tables 1–4

Enchelyopus bachus Forster in Bloch and Schneider, 1801: 53. Type locality: Queen Charlotte Sound, New Zealand. No types known. Based on manuscript description of *Gadus bacchus* by Forster.

Gadus bacchus. Cuvier, 1817: 486; Forster in Lichtenstein, 1844: 120, 420; Whitehead, 1978: 40; Hoare, 1982: 269.

Lota bacchus Cuvier, 1829: 334; Richardson, 1846: 61.

Brosmius venustus Richardson and Gray, 1843: 222 (generic referral of Parkinson's unpublished manuscript name *Blennius venustus*, written on the painting used by Forster for his description of *Gadus bacchus*). Richardson, 1843: 27; Taylor, 1855: 413.

Enchelyopus bacchus. Lichtenstein, 1844: 419 (index only).

Lotella bacchus. Günther, 1862; 347; Hutton and Hector, 1872: 46, 115; Hector, 1875: 239; Hector, 1884: 55; Hector, 1886: 28; Hutton, 1875: 134; Thomson, 1877: 485; Thomson, 1878: 326; Thomson, 1879: 382; Dambeck, 1879: 536, 547, 555; Parker, 1882: 263; Parker, 1883: 234, 235, pl. 33; Sherrin, 1886: 16, 17, 93, 304; Thomson, 1890: 370, pl. 28; Beattie, 1891: 71, 81, 82, pl. 12, pl. 13, pl. 14, pl. 15; Thomson, 1892: 212; Ayson, 1900: 14; Mair, 1903: 319; Ayson, 1907: 22; Johnson, 1921: 473; Carter and Malcolm, 1926: 647; Malcolm, 1926: 658; Svetovidov, 1937: 1285; Svetovidov, 1948: 17, 60 (anatomy).

Pseudophycis bacchus. Günther, 1880a: 26 (Port Hardy, D'Urville Island); Murray, 1895: 599 Gill, 1893: 94, 95 100, 120 (list); Karrer, 1971: 153, 179, 180, 185, 195; Habib, 1975: 1; Ayling and Cox, 1982: 142, pl 9. (description).

Pseudophycis bachus. Günther, 1880b: 542–543, fig. 248; Ogilby, 1886: 48 (list, in part); Hutton, 1890: 282; Fitch, 1972: 570, 573; Marshall and Cohen, 1973: 490; Edgar et al., 1982: 32, fig. 17 (description, in part); Paulin, 1983: 91 (description, taxonomy, in part); Paulin and Stewart, 1985: 22; Paul, 1986: 57, fig. (in part); Francis 1988: 21, pl. 18; Paulin, 1988: 450, 451, 453; Paxton and Hanley in Paxton et al., 1989: 302 (list, in part); Paulin et al., 1989: 119 (keyed), 255 (list); Cohen in Cohen et al., 1990: 373 (taxonomy, in part); Paulin in Amaoka et al., 1990: 155, fig. 103 (description, in part); Paulin and Roberts, 1992: 130, fig. 62a (description, in part); Kuiter, 1993: 59 (description, in part); Gomon in Gomon et al., 1994: 333 (description, in part); Francis, 1996: 20, pl. 18; Horn, 1996: 151, 158; Kuiter, 1997: 50 (description, in part); Paulin, 1998: 52, fig. (description); Paul, 2000: 57 (description); Francis, 2001: 25, pl. 19; Beentjes and Renwick, 2001: 315, 316; Paxton et al., 2006: 616 (taxonomy, in part); Hirt-Chabbert, 2006: 39; Gomon in Gomon et al., 2008: 313 (description, in part); Roberts et al., in Gordon et al., 2009: 532 (listed); McMillan et al., 2011a: 161, 162; McMillan et al., 2011b: 94; Francis, 2012: 5; Horn et al., 2012: 624, 625, 627–629, 631–633; Roberts et al., 2014: 18 (listed); Struthers et al., in Roberts et al., 2015: 864, fig. 107.20 (description); Roberts et al., 2015: S164 (listed); Roberts et al., 2017: 81 (listed), Roberts et al., 2019: 90 (listed).

Physiculus bacchus. Günther, 1887: 87; Goode and Bean, 1895: 365, 549; Hutton, 1896: 316; Hutton, 1904: 48 (listed); Thomson, 1906: 551; Thomson and Anderton, 1921: 74; Thomson and Thomson, 1923: 111; Frost, 1924: 609; Frost, 1926: 488, 490; Young, 1925: 370; Archey in Speight, Wall and Laing, 1927: 203; Anonymous, 1931: 32; Frost, 1933: 140; Benham, 1934: 31; Benham, 1935: 22; Benham, 1938: 56; Graham, 1938: 405; Graham, 1939: 364; Doogue and Moreland, 1960: 197, 288; Doogue and Moreland, 1961: 208, 316; Moreland, 1963: 20; Webb, 1966: 52, fig. 2.8, 70, 128, table 3.4, 164, 209, 230, 231, 234, 238–240, 257, 263, 266, 280, 294b, 294c; Webb, 1972b: 43; Webb, 1973: 307–309; Heath and Moreland, 1967: 37, 56; Whitehead, 1969: pl. 11; Anonymous, 1971: 17; Anonymous, 1972c: 47; Watkinson and Smith, 1972: 31; Knox and Kilner, 1973: 354; Vooren, 1974: 43, 44.

Physiculus bachus. Stead, 1906: 86 (in part); Waite, 1907: 18 (listed); Zietz, 1909: 266; Waite, 1909: 51, 52, 57, 134; Waite, 1911: 162, 183, 259, 265, 270, pl. 31; Thomson, 1913: 233; Phillipps, 1918: 271; Phillipps, 1921: 121, 125; Phillipps and Hodgkinson, 1922: 95; Waite, 1923: 92 (in part); Ayson, 1924: 7; Lord and Scott, 1924: 8, 43; Phillipps, 1926: 528; Lord, 1927: 13; Phillipps, 1927a: 128; Phillipps, 1927b: 23, 60; Phillipps, 1927c: 12; Waite, 1928: 6 (listed); McCulloch, 1929: 129 (in part); Young, 1929: 141; Anonymous, 1930: 28; Finlay, 1930: 47; Anonymous, 1934: 43; Anonymous, 1935: 34; Norman, 1935: 3; Benham, 1936: 26; Hefford, 1936: 71, 74; Cunningham, 1937: 898, Norman, 1937: 54, 55 (in part, listed); Shorland, 1937: 223; Wilson, 1937: 31; Johnston, 1938: 47; Munro, 1938: 62; Graham, 1939b: 364; Fowler, 1940: 758; Rapson, 1940: 35; Phillipps, 1947: 42; Phillipps, 1948: 129; Shorland, 1948: 109; Laird, 1949: 14, 19, 36, 37, 39, 53, 56, 60, 61, 137, 145, 146; Phillipps, 1949: 24, 59; Shorland, 1950: 35; Laird, 1951: 287, 298, 306, 308; Laird, 1952: 589, 590, 595, 596, 600; Graham, 1953: 166, 173, 399; Manter, 1954. 498, 545, 547, 549, 559; Robinson, 1955: 10, 71, 105, pls 9 and 14; Anonymous, 1957: 69; Kaberry, 1957: 90; Moreland, 1957: 34, 36; Parrott, 1957: 47, 175; Anonymous, 1958: 73; Parrott, 1958: 117; Anonymous, 1959: 70;

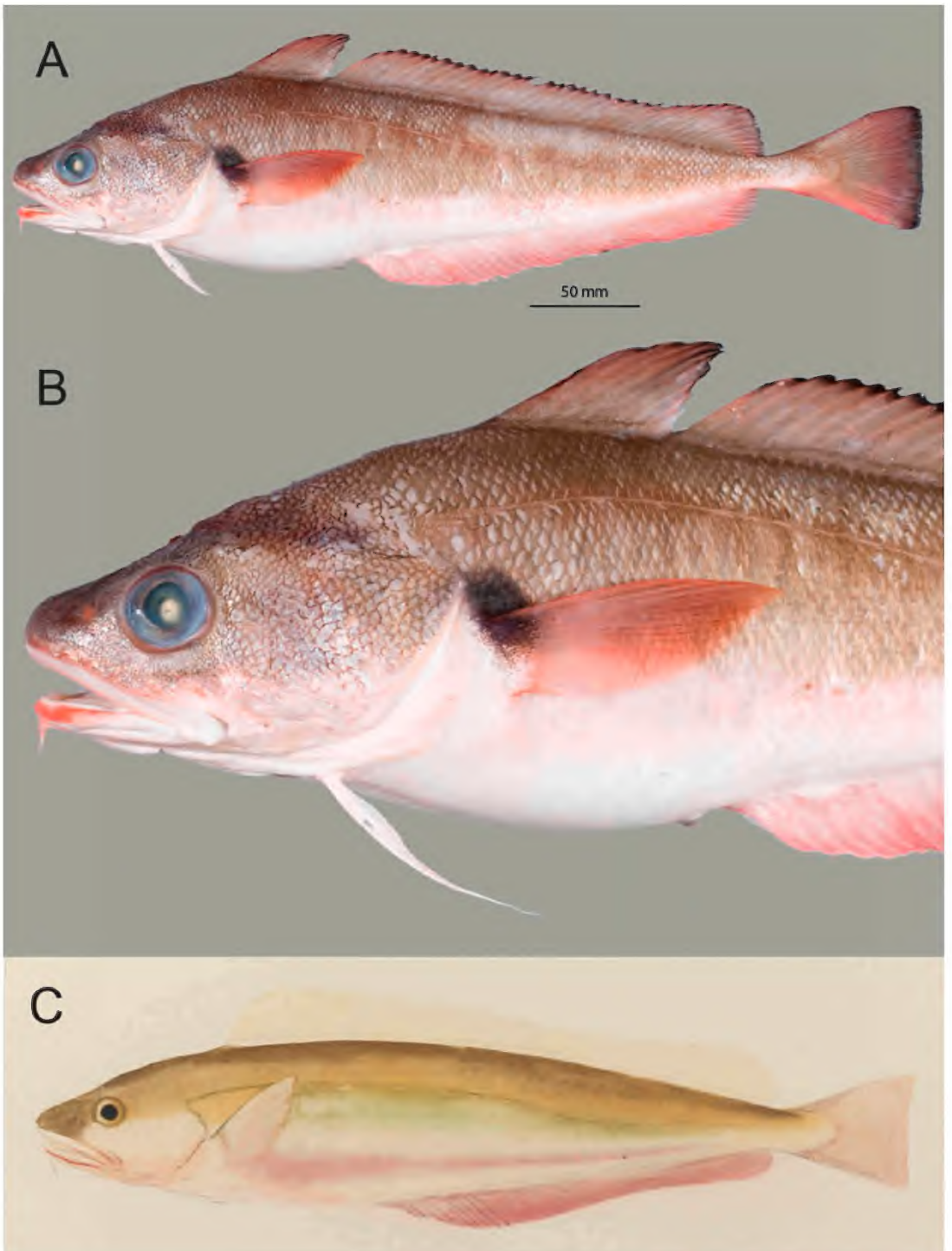

Figure 6. *Pseudophycis bachus.* A, B, NMNZ P.054828, neotype, 351 mm SL, 2.5 km off coast from Whanganui River bar, Whanganui, New Zealand, fresh specimen, lateral view of body and anterior body showing black pectoral blotch respectively (photographs C. Struthers, NMNZ); C, unpublished line drawing by S. Parkinson of *Enchelyopus bachus* Forster in Bloch and Schneider, 1801 (reproduced from Whitehead, 1969: pl. 31).

Robinson, 1959: 152; Anonymous, 1960: 70; Parrott, 1960: 67, 164; Meglitsch, 1960: 321–323; Scott, 1962: 84 (in part); Gorman, 1963: 29; Graham, 1963: 167; Doogue and Moreland, 1964: 205, 311; Street, 1964: 18; Anonymous, 1965: 15, 22; Churchman, 1965: 56; Doogue and Moreland, 1966: 205, 311; Elder, 1966: 96, 97; Howell, 1966: 33; Paul, 1966: 372, 373; Svetovidov, 1967: 1685, 1686, 1689, 1690; Sorensen, 1968: 148; Tong and Elder, 1968: 64; Doogue and Moreland, 1969: 205, 311; Russell, 1969: 108; Cowper, 1970: 45; Godfriaux, 1970: 257; Iwai et al., 1970: 21; Shuntov, 1970: 373, 374, 376; Sorensen, 1970: 4, 17; Coakley, 1971: 24; Russell, 1971a: 9, 19, 21, fig. 3, 38, 41, 94, 173, table 10, fig. 13, 191, 197; Russell, 1971b: 83; Anonymous, 1972a: 229; Anonymous, 1972b: 187–189, 278; Doak, 1972: 19, 101, 131; Hewitt and Hine, 1972: 92; Iwai et al., 1972: 29, 36; Shuntov, 1972: 339; Walker, 1972: 2; Webb, 1972a: 16; Suda, 1973: 2150–2152; Waugh in Williams, 1973: 257, 274; Williams, 1973: 427; Godfriaux, 1974: 502; Ryan, 1974: 133, 135; Scott et al., 1974: 95, 96 (in part).

Lotella bachus. Ayson, 1908: 28; Rendahl, 1926: 2.

Physiculus backus. Fowler, 1940: 758 (near Loba, New Zealand).

Physiculus (Pseudophycis) bachus. Graham, 1956: 166; Whitley, 1956: 403; Whitley, 1968: 40 (list).

Pscudophycis bachus. Doogue and Moreland, 1982: 218, fig. (misspelling).

Diagnosis. First dorsal fin 11–13 rays, second dorsal fin 40–45 rays; anal fin 42–48 rays; total vertebrae 44–46; scales above lateral line in oblique series from base of first dorsal fin ray 10–12; oblique rows of scales intersecting with lateral line 102–136; pyloric caeca 6; caudal peduncle moderately short 28.0–38.9% HL; barbel short, 8.6–16.9% HL; caudal fin truncate with angular corners in specimens larger than about 150 mm SL, middle rays shorter than rays extending to corners; dark blotch basally on pectoral fin extending well onto side above fleshy pectoral fin base; underside of head and body whitish; anal fin mostly whitish with faint narrow black distal margin only posteriorly, if at all. A large species reaching at least 650 mm SL.

Description. (Values for neotype with those for non-type specimens when different in parentheses; see Tables 2–4 for summary of selected meristic and comparative morphometric values.) First dorsal fin 11 (11–13, rarely 13, first ray usually minute); second dorsal fin 42 (40–45, usually 42 or 43); anal fin 45 (42–48, usually 45–47); pectoral fin 24 (22–25, rarely 22); pelvic fin 5; caudal fin 36 (33–39); gill rakers 4 + 10 (4–5 + 10–12 = 14–16); lateral line pores not associated with individual scales; oblique scale rows intersecting with lateral line 112 (102–136); scales in oblique series above lateral line 11 (10–12), scales in oblique series below lateral line 30 (26–34, rarely 33 or 34); vertebrae 16 + 29 (16–17 + 27–30 = 44–46); pyloric caeca 6.

Body moderately slender, compressed laterally (fig. 6), greatest depth at anal fin origin 19.5 (18.4–23.7)% SL, tapering uniformly from second dorsal fin origin to shallow caudal peduncle; caudal peduncle short, 8.5 (7.7–10.5)% SL, strongly compressed, depth less than orbital diameter. Distance between middle of anus and base of anal fin less than suborbital depth. Body cavity extending posteriorly to above origin of anal fin.

Head acute, of moderate size, length 26.5 (25.9–29.6)% SL, its width 14.4 (13.4–17.7)% SL and depth 11.7 (10.2–15.6)% SL; snout of moderate length 7.5 (7.1–9.0)% SL, not projecting in advance of upper jaw, rounded in dorsal view. Nostrils small, located about two-thirds to three-quarters of the way from snout tip to eye, distance from nostril to orbital margin equal to or greater than diameter of combined nostrils; nostrils positioned above horizontal through centre of eye; posterior opening larger than anterior, separated from it by raised skin flap; posterior opening with tubular flap encircling margin. Interorbital of moderate width, very slightly convex. Eye of moderate size, orbital diameter 21.1 (17.0–30.4)% HL, 1.58 (0.98–2.00) times in interorbital space, 2.20 (1.50–4.25) times suborbital distance, circular, upper edge of eye adjacent to dorsal margin of head in lateral view, transparent skin covering eye faintly pigmented near orbital dorsal margin. Postorbital moderately long, 1.01 (0.89–1.22) times length of upper jaw. Mouth large, terminal, upper jaw terminating at vertical through posterior margin of eye. Jaw teeth caniniform, slightly curved, depressible, band of up to four or five irregular rows in upper jaw with distinct hiatus at symphysis; teeth in outer row more regularly arranged than in inner rows; band tapering near rear of jaw. Teeth of lower jaw similar in form to those of upper jaw; band of two or three rows with broader patch on either side of symphysis, tapering to single, widely spaced row posteriorly; rows almost contiguous across symphysis. Vomerine teeth absent. Opercular bones strong; upper extremity of gill opening at horizontal through middle of eye; gill membranes continuous across isthmus. Gill rakers on outer arch slender, of moderate length, almost as long near angle as opposing gill filaments, 12.8 (9.5–12.8) times in head, their inner margin denticulate. Chin barbel short, subconical 12.0 (8.6–16.9)% HL.

Small cycloid scales covering all of head, including isthmus and gular region, and body except for branchiostegal membranes, surface of maxilla and premaxilla, lower lip and distal parts of fins; thick mucus covering obscuring scales and pores in freshly preserved material. Most head pores tiny, following main cephalic sensory canals; row of slightly raised pores from nostrils to tip of snout and then posteriorly just above lower edge of suborbital; row of enlarged mandibular pores on underside of lower jaw. Lateral line comprising widely spaced pores on short tubes arising from narrow scaleless gap, anterior end curved upwards slightly, then gradually descending to lateral midline below posterior 25% of second dorsal fin, remaining on lateral midline posteriorly.

Membranes of first and second dorsal fins continuous at base; first dorsal originating vertically above pectoral fin base; anterior two-thirds of second dorsal of uniform height, 7th to 9th ray from posterior end of fin longest, its height about 1.4 times length of 2nd ray at anterior end of fin, subsequent rays progressively shorter; rays of both dorsal fins mostly unbranched, only last 13 to 16 rays of second dorsal, apart from last one to three, branched. Fleshy, fine scale-covered basal sheath on third or more of first dorsal and anterior portion of second dorsal fins; fin rays interconnected by membranes to tips, sheath gradually decreasing in coverage and thickness posteriorly, encompassing about half of second dorsal fin near its insertion; sheath extending onto body for anterior third of combined dorsal fin base, broadest anteriorly, narrowing posteriorly. Profile of anal fin like that of second

dorsal fin, although shallower posteriorly, with comparable unbranched and branched rays. Likewise, anal fin enclosed in broad fleshy sheath that is like that of dorsal fins; sheath also extending onto body for anterior third or less of fin. Caudal fin truncate with distinct dorsoposterior and ventroposterior corners in adults, posterior margin with little if any convex curve; longest rays to corners, middle rays about 85–90% length of longest rays; fin more rounded in juveniles; base of fin covered by indistinct sheath sharply demarcated from scales of caudal peduncle. Pectoral fin tip variably reaching almost to, to or past vertical through anal fin origin, sixth or seventh ray longest. Pelvic fin inserted anterior to vertical through posterior edge of preopercle (more posteriorly in some specimens); outer two rays longer than inner rays; second ray longest, 16.0 (11.5–21.1)% SL, nearly twice length of subsequent ray, reaching past a vertical through first dorsal fin origin.

Fresh colour. (Based on images of neotype; fig. 6A, B.) Medium brown above extending ventrally to level of ventral edge of pectoral fin base, white below, suffused with pinkish hue, especially above anal fin base; lateral line slightly paler at least anteriorly. Underside of head, jaws and barbel white, tinged with pink. Dorsal and caudal fins medium brown, caudal paler with reddish tinge ventrally; anal fin white with pink hue; dorsal fins with fine black distal margin; caudal fin margin with broader, more diffuse black margin; anal fin with faint black distal margin, darkest posteriorly. Pectoral fin medium brown with semi-circular black basal spot covering dorsal half of fin edge proximally, extending well onto side of body above fin base; ventroposterior margin of fin pale to translucent. Pelvic fin rays white with pink hue.

Preserved colour. Upper half of head and body pale dusky to dusky, lower half very pale, frequently pearly white. Dorsal and caudal fins pale dusky; distal edge of dorsal fin with fine dark margin; posterior edge of caudal fin broadly dark; anal fin very pale, distal edge of fin posteriorly with fine dark margin in some; pelvic fin, pectoral fin and basal half of anal fin very pale; pectoral fin with prominent dark spot covering dorsal half or more of basal edge that extends onto side above pectoral fin base.

Etymology. The name *bachus* is an altered spelling of *bacchus*, the Greek god of wine, adopted for the wine-red colouration assumed shortly after capture but lost soon after death.

Distribution. Endemic to New Zealand, occurring around both the North and South Islands, and reaching the Chatham Islands in the east (fig. 3A). A demersal species on soft bottom at 2–570 m depth.

Remarks. Pseudophycis bachus was originally described as *Enchelyopus bachus* Forster in Bloch and Schneider, 1801, based on Forster's manuscript description of "Gadus bachus", subsequently published by Lichenstein (1844: 120). Forster's drawing No. 180, on the back of which is pencilled "ex Queen Charlotte Sound", is evidently an illustration of the fish on which the description was based. Although both Bloch and Schneider (1801: 53) and Lichtenstein gave the origin of the specimen simply as "in the seas around New Zealand", Whitehead (1969: pl. 11), Paulin (1983: 91) and Fricke et al. (2019) regarded Queen Charlotte Sound, the presumed collection locality of the specimen implied in the note on Forster's illustration, as the type locality. However, Hoare's (1982: 269) reproduction of *Forster's Resolution Journal* has a footnote stating "Gadus bacchus of Descr. Anim., p. 120 and Forster drawing 180 (undated). The description is from a specimen of 22 inches (559 mm), dated 13 April 1773". That date puts the type locality as Dusky Sound from a larger fish. Paulin (1983: 92) provided a detailed discussion of the origin and various iterations of Bloch and Schneider's name.

An unfinished drawing by Parkinson (vol. 2, no. 5, ex Totarra 'nue, 404 mm tot. l.) reproduced by Whitehead (1969: pl. 11; here as fig. 6C), has "*18, Blennius venustus*" pencilled on the reverse side and is the basis for Richardson and Gray's (1843: 222) *Brosmius venustus*. The fish figured is clearly an example of *P. bachus*, despite the incomplete nature of the illustration. Totaranui is the Maori name for Queen Charlotte Sound. The scientific name is regarded as unavailable because no distinguishing features were provided by the authors (Fricke et al., 2019). The illustrated characters agree with those of specimens from New Zealand identified as *P. bachus*.

Because no type specimen of *P. bachus* is known (Fricke et al., 2019), the designation of a neotype for *P. bachus* is considered justified. A specimen (NMNZ P.054828, 351 mm SL; fig. 6a) collected from 2.5 km off the coast from Whanganui River bar, Whanganui, New Zealand, is proposed as the neotype for *P. bachus*. Accordingly, Whanganui, New Zealand, becomes the type locality of *P. bachus* under Article 76.3 (ICZN, 1999), replacing the original type locality Queen Charlotte Sound, New Zealand.

Material examined. Neotype. NMNZ P.054828† (351) 2.5 km off the coast from Whanganui River bar, Whanganui, New Zealand, 39° 53' S, 174° 49' E, 18 m, C. Papple, 10 October 2012.

Other material. (38 non-type specimens examined for meristic or morphometric values, 110–539 mm SL; see Appendix 2 for additional material in Australasian collections.) **New Zealand, *North Island*:** NMNZ P.001718 (539) off Castlepoint, Wairarapa, 40° 54' S, 176° 13' E, 73–110 m, F. Abernethy, 8 July 1955; NMNZ P.033899 (5, 121–202) off Raglan, Waikato, 37° 48.33' S, 174° 34.00' E, RV Kaharoa, 61–63 m, 26 October 1996. ***South Island:*** NMNZ P.025037 (2, 479–512) Blueskin Bay, Otago Peninsula, Otago, 45° 43.28' S, 170° 40.33' E, 20–22 m, C.D. Roberts and C.D. Paulin, 9 May 1990; NMNZ P.025129 (4, 137–192) Entrance mole, Otago Harbour, Otago, 45° 46.45' S, 170° 43.23' E, 6–9 m, C.D Roberts, 9 May 1990; NMNZ P.027580 (239) Harrold's Bay, Halfmoon Bay, Stewart Island, 46° 53.75' S, 168° 9.25' E, 2–5 m, NMNZ Stewart Island field team, 4 March 1992; NMNZ P.032385 (2, 328–395) Mooring, head of Gold Arm, Charles Sound, Fiordland, 45° 8.55' S, 167° 8.78' E, 5–10 m, NMNZ Fiordland 1995 field team, 24 March 1995; NMNZ P.032393 (3, 292–309) Mooring at Toe Cove, head of Nancy Sound, Fiordland, 45° 10.55' S, 167° 8.85' E, 25 m, NMNZ Fiordland 1995 field team, 26 March 1995; NMNZ P.035991 (388) Flowerpot Rock, Jackson's Bay, West Coast, 43° 58.03' S, 168° 37.30' E, 5–8 m, NMNZ Jackson-Haast 1999 field team, 7 February 1999; NMNZ P.044338† (136) south of Timaru, Canterbury, 44° 45.04' S, 171° 18.40' E, 26–31 m, RV Kaharoa, 3 June 2007; NMNZ P.044339† (176) south off Timaru, Canterbury, 44° 45.04' S, 171° 18.40' E, 26–31 m, RV Kaharoa, 3 June 2007; NMNZ P. 047709 (229) Lyttelton Port, Canterbury, 43° 36.33' S, 172° 43.10' E, NIWA

Port Survey, 4 November 2004; NMNZ P.049392 (343) c. 7 km east-north-east of Kaikoura Peninsula, 42° 24.77' S, 173° 48.22' E, 93 m, C.D. Struthers, 16 November 2010; NMNZ P.049401 (370) c. 6 km north-east of Kaikoura Peninsula, 42° 23.60' S, 173° 47.59' E, 49 m, C.D. Struthers, 16 November 2010; NMNZ P.049402 (545) c. 5 km east-south-east of Kaikoura Peninsula, 42° 26.77' S, 173° 46.39' E, 94 m, C.D. Struthers, 17 November 2010; NMNZ P.049403 (519) c. 5 km south off Kaikoura Peninsula, 42 28.09' S, 173 43.02' E, 91 m, C.D. Struthers, 19 November 2010; NMNZ P.049406 (485) and NMNZ P.049407 (467) c. 3 km south off Kaikoura Peninsula, 42° 24.72' S, 173° 45.22' E, 47 m, C.D. Struthers, 17 November 2010; NMNZ P.049678 (358) Bay View, end of Franklin Road, Hawke's Bay, 10–15 m, C.D. Struthers and D.H. Struthers, 27 December 2010; NMNZ P.052508 (297) and NMNZ P.052509 (290) south of Pegasus Canyon mouth, Canterbury Bight, 43° 33.99' S, 173° 33.44' E, 86 m, RV Tangaroa, 13 May 2011; NMNZ P.053748† (383), NMNZ P.053749† (405), NMNZ P.053750† (368), NMNZ P.053751† (373) and NMNZ P.053752† (337) Port Pegasus; Stewart Island, 47° 13.20' S, 167° 41.38' E, 64 m, C.D. Struthers, 20 February 2012. ***Chatham Rise:*** NMNZ P.044348† (273) central Chatham Rise, 43° 47.42' S, 179° 30.01' W, 327–328 m, RV Tangaroa, 31 December 2007; NMNZ P.044349† (382) central Chatham Rise, 43° 47.42' S, 179° 30.01' W, 327–328 m, RV Tangaroa, 31 December 2007; NMNZ P.044350† (297) central Chatham Rise, 43° 43.78' S, 179° 24.00' W, 367–375 m, RV Tangaroa, 31 December 2007.

Pseudophycis barbata Günther 1862

Common name: Bearded Rock Cod (Australian Standard); southern bastard cod (New Zealand)

Figures 1, 3B, 4, 5, 7; Tables 1–4

Pseudophycis barbatus Günther, 1863: 116. Type locality: Victoria, South Australia. Holotype: BMNH 1863.1.15.38 (skin in alcohol).

Pseudophycis barbatus. McCoy, 1878: 29, pl. 20 (in part, description); Johnston, 1883: 126 (description); Ayling and Cox, 1982: 144, fig. (description).

Lotella grandis Ramsay, 1881: 462. Type locality: Wollongong, New South Wales. Holotype: AMS I.696 (decision by Paulin, 1983: 94).

Lotella grandis. Steindachner, 1901: 509 (description).

Physiculus barbatus. Zietz 1909: 266; Waite, 1923: 91, fig. (description); Lord and Scott, 1924: 8, 43 (description); McCulloch, 1927: 32 (listed); Waite, 1928: 6 (listed); McCulloch, 1929: 128 (list); Norman, 1937: 55 (listed); Munro, 1938: 62, fig. 440 (description); Whitley, 1955: 119 (taxonomy); Scott, 1962: 84, fig. (description); Whitley, 1964: 40 (list); Svetovidov, 1967: 1686; Scott et al., 1974: 95, fig. (description).

?*Pseudophycis breviusculus* (nec Richardson, 1846) Graham, 1939: 405 (after Paulin, 1983: 93).

Pseudophycis breviusculus (nec Richardson 1846). Habib, 1975: 32–57.

Physiculus (Pseudophycis) breviculus (nec Richardson, 1846). Graham, 1956: 173 (in part, locality implies multiple species; misspelling).

Physiculus (Pseudophycis) breviusculus (nec Richardson, 1846) Whitely, 1956: 403 (in part?).

Pseudophycis barbata. Paulin, 1983: 94, fig. 10 (description, new record for NZ); Paulin and Stewart, 1985: 22; Hutchins and Swainston, 1986: 34 124, fig. 114 (description); May and Maxwell, 1986: 195 (description); Paul, 1986: 58, fig; Francis, 1988: 21, pl. 19; Paulin, 1988: 453; Paxton and Hanley in Paxton et al., 1989: 302 (list); Paulin et al., 1989: 119 (key), 255 (listed); Cohen in Cohen et al., 1990: 374 (taxonomy); Paulin in Amaoka et al., 1990: 156 (description); Kuiter, 1993: 59 (description); Gomon in Gomon et al., 1994: 334 (description); Francis, 1996: 21, pl. 19; Horn, 1996: 157; Kuiter, 1997: 50 (description); Paulin, 1998: 67, fig. (description); Paul, 2000: 58; Francis, 2001: 25, pl. 18; Hutchins, 2001: 23 (description); Paxton et al., 2006: 616 (list); Hirt-Chabbert, 2006: 40; Gomon in Gomon et al., 2008: 314 (description); Roberts et al. in Gordon et al., 2009: 532 (listed); McMillan et al., 2011a: 161, 162; McMillan et al., 2011b: 94; Francis, 2012: 52; Roberts et al., 2014: 18 (list); Struthers et al. in Roberts et al., 2015: 863, fig. 107.21 (description); Roberts et al., 2015: S164; Roberts et al., 2017: 81 (list), Roberts et al., 2019: 90 (listed).

Diagnosis. First dorsal fin with 10–11 rays, second dorsal fin with 54–59 rays; anal fin with 54–63 rays; total vertebrae 48–51; scales above lateral line in oblique series from base of first dorsal fin ray 16–22; oblique rows of scales intersecting with lateral line 123–162; pyloric caeca 14–20; caudal peduncle short 13.5–18.6% HL; chin barbel of moderate length, 16.5–35.1% HL; caudal fin rounded without angular corners, the middle rays equal to or longer than rays above and below; no distinct, dark blotch basally on pectoral fin although fin base sometimes overall dark; underside of head and body tan to brown; anal fin tan to brown with distinct black distal margin. A large species reaching at least 620 mm SL.

Description. (Values for non-type specimens when different from type in parentheses; see Tables 2–4 for summary of selected meristic and comparative morphometric values.) First dorsal fin 10 (10–11), first ray small to minute; second dorsal fin 59 (54–59, rarely 59); anal fin 59 (54–63); pectoral fin 25 (24–27, rarely 24); pelvic fin 5; caudal fin 33 (32–35 rays); gill rakers unknown (3–4 + 8–11 = 12–14); lateral line pores not associated with individual scales; oblique scale rows intersecting with lateral line unknown (123–162); scales in oblique series above lateral line unknown (16–22), scales in oblique series below lateral line unknown (38–56, rarely less than 45); vertebrae unknown (14–16 + 33–37, rarely 37 = 48–51); pyloric caeca unknown (14–20).

Body of moderate depth, moderately compressed laterally (fig. 7b), greatest depth at anal fin origin unknown (19.7–29.3)% SL, tapering uniformly from second dorsal fin origin to shallow caudal peduncle; caudal peduncle short, 5.4 (5.2–9.2)% SL, strongly compressed, depth subequal to orbital diameter. Distance between middle of anus and base of anal fin slightly less than suborbital depth. Body cavity extending to above origin of anal fin.

Head acute, of moderate size, length 23.3 (23.3–31.6)% SL, width unknown (14.9–19.8)% SL and depth unknown (11.0–17.9)% SL; snout of moderate length 7.5 (6.5–9.6)% SL, not projecting in advance of upper jaw, rounded in dorsal view. Nostrils small, located about two-thirds to three-quarters of the way from snout tip to eye, distance from nostril to orbital margin about equal to or greater than diameter of combined nostrils; nostrils positioned above horizontal through centre of eye, both with low tubular rim; posterior opening about half size of anterior, separated from it by raised skin flap. Interorbital of moderate width, very slightly convex. Eye of moderate size, orbital diameter 20.8 (16.8–28.5)% HL, unknown (0.91–1.68) times in interorbital space, unknown (1.46–4.71) times suborbital distance, circular, upper edge of eye adjacent to

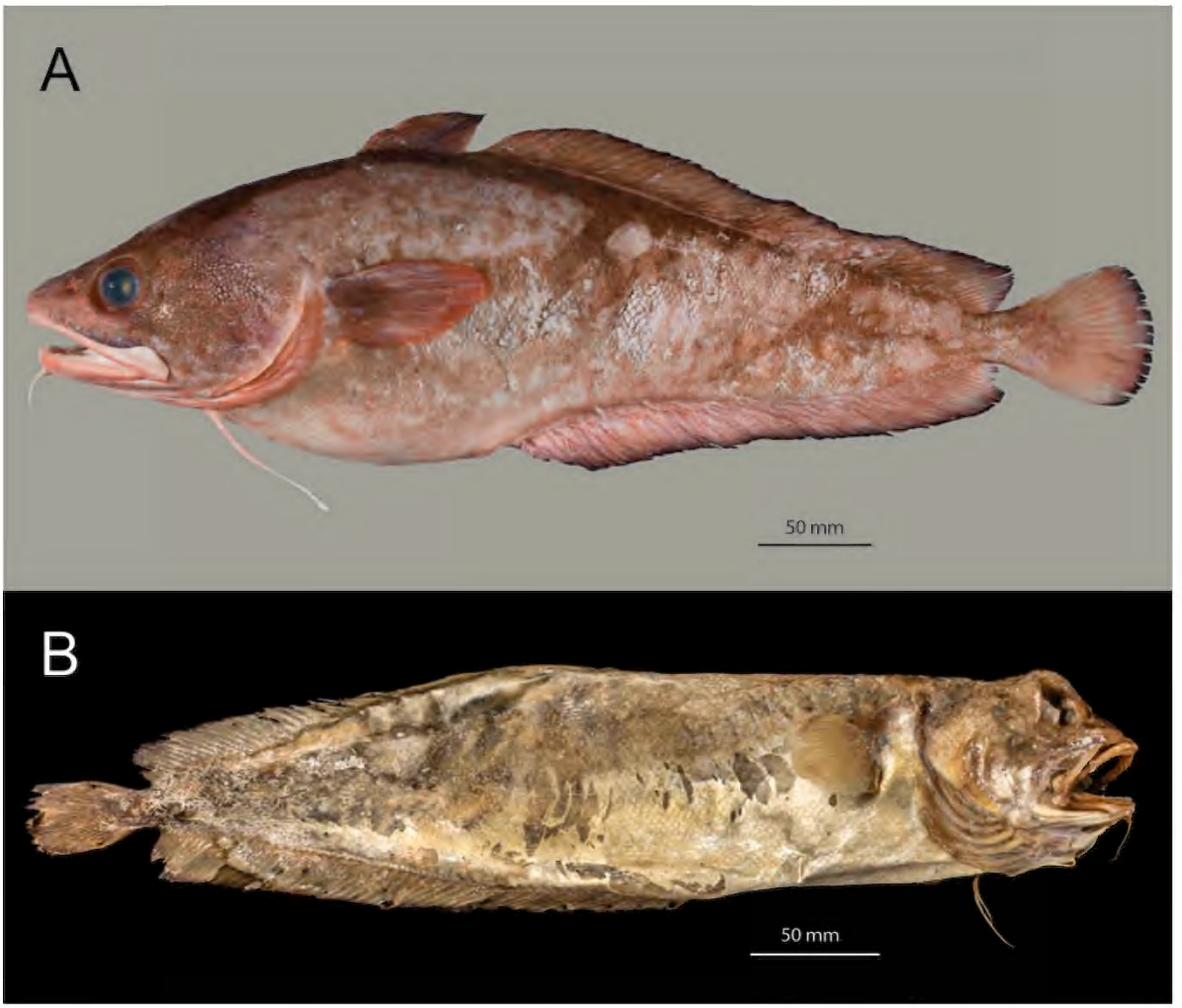

Figure 7. *Pseudophycis barbata*. A, NMNZ P.037124, 450 mm SL, Bay of Plenty, east of north-east point, North Island, New Zealand (photograph C. Struthers, NMNZ); B, BMNH 1863.1.15.38, holotype of *Pseudophycis barbata*, 394 mm SL, Victoria, South Australia (photograph © The Trustees of the Natural History Museum, London).

dorsal margin of head in lateral view. Postorbital moderately long, 1.00 (0.52–1.21) times length of upper jaw. Mouth large, terminal, upper jaw terminating at vertical through posterior margin of eye. Jaw teeth caniniform, slightly curved, depressible, band of up to four or five irregular rows in upper jaw with distinct hiatus at symphysis; teeth in outer row more regularly arranged than in inner rows; band tapering near rear of jaw. Teeth of lower jaw similar in form to those of upper jaw; band of two or three rows with broader patch on either side of symphysis, tapering to single, widely spaced row posteriorly; rows almost contiguous across symphysis. Vomerine teeth absent. Opercular bones strong; upper extremity of gill opening at horizontal through middle of eye; gill membranes continuous across isthmus. Gill rakers on outer arch slender, moderately short, unknown (about 0.6–0.8) times length of opposing gill filaments near angle, unknown (19–22) times in head length, slightly denticulate. Chin barbel of moderate length, subconical 21.1 (16.5–25.3)% HL.

Very small cycloid scales covering all of head and body except for branchiostegal membranes, surface of maxilla and premaxilla, lower lip and distal parts of fins; thick mucus covering obscuring scales and pores in freshly preserved material. Most head pores tiny, following main cephalic sensory canals; row of slightly raised pores from nostrils to tip of snout and then posteriorly just above lower edge of suborbital; row of enlarged mandibular pores on underside of lower jaw. Lateral line comprising widely spaced pores on short tubes arising from narrow scale-less gap, anterior end

curved upwards slightly, then gradually descending to lateral midline below posterior 25% of second dorsal fin, remaining on lateral midline posteriorly.

Membranes of first and second dorsal fins continuous at base; first dorsal originating distinctly behind vertical through pectoral fin base; anterior two-thirds of second dorsal of uniform height, 7th to 9th ray from posterior end of fin longest, its height about 1.4 times length of 2nd ray at anterior end of fin, last ten or so rays progressively shorter; rays of both dorsal fins mostly unbranched, only last 13 to 16 rays, apart from last one to three, branched. Fleshy, fine scale-covered basal sheath on third or more of first dorsal and anterior portion of second dorsal fins; fin rays interconnected by membranes to tips, sheath gradually decreasing slightly in coverage and thickness posteriorly, encompassing about half of second dorsal fin near its insertion; sheath extending onto body for anterior third of combined dorsal fin base, broadest anteriorly, narrowing posteriorly. Profile of anal fin like that of second dorsal fin, although less deep posteriorly, with comparable unbranched and branched rays. Likewise, anal fin enclosed in broad fleshy sheath that is like that of dorsal fins; sheath also extending onto body for anterior third or less of fin. Caudal fin distinctly rounded without obvious dorsoposterior and ventroposterior corners in adults; all but anterior-most rays of similar length; base of fin covered by indistinct sheath with much smaller scales (sheath sharply demarcated from scales of caudal peduncle). Pectoral fin tip variably reaching not quite to, or past vertical through anal fin origin, sixth or seventh ray longest. Pelvic fin inserted anterior to vertical through posterior edge of preopercle; outer two rays longer than inner rays; second ray longest, 13.3 (13.3–24.9)% SL, nearly twice length of subsequent ray, reaching vertical through first dorsal fin origin.

Fresh colour. (Based on images of non-type material; fig. 7A.) Medium to dark reddish brown above, extending ventrally to level of ventral portion of pectoral fin base, white below in smaller individuals, large individuals becoming brown ventrally and often much darker; lateral line not distinctively coloured. Underside of head, jaws and barbel white, tinged with pink to orange, becoming more orange to brown in larger individuals; ventral margin of suborbital dusky to dark. Dorsal and caudal fins of similar colour to brown of sides, anal fin pink or orange in smaller individuals, becoming brown like other median fins in large individuals, dorsal, caudal and anal fins with distinct broad to narrow black margin distally, margin on caudal fin broadest. Pectoral fin orange to brown with faintly darker semi-circular brown blotch basally, covering dorsal 80% of edge of fin proximally. Pelvic fin rays white with pink to orange hue, becoming brownish in large individuals.

Preserved colour. Head and body dusky to dark dusky; underside of head, belly and side adjacent to anal fin pale, especially in small specimens, extent of pale underside less in large individuals. Dorsal, caudal and anal fins dusky to dark dusky, anal fin often less dark than dorsal and caudal; distal edges of dorsal, caudal and anal fins with distinctly dark margins, dark margin on caudal fin broad; pectoral fin broadly dusky basally, becoming pale toward outer margin. Pelvic fin pale dusky.

Etymology. The specific epithet *barbatus* is Latin for "bearded" in reference to the chin barbel, which is characteristic of this species, its congeners and many other members of the family.

Distribution. Endemic to coastal waters of Australia and New Zealand from Rottnest Island, Western Australia (32° 01' S, 115° 30' E), to Port Stephens, New South Wales (32° 30' S, 152° 35' E), including all of Tasmania and around both the North and South Islands of New Zealand, reaching the Chatham Islands in the east (fig. 3B). A demersal species on rocky bottom at 1 to at least 520 m. Although found at considerable depths in New Zealand waters, this is a shallow reef-dwelling species in southern Australia, where it shelters in caves and beneath overhangs during daylight hours, venturing out at night to feed.

Remarks. Pseudophycis barbata has an overall darker colouration than its congeners, often with a reddish hue in fresh material, and distinct black margins to the dorsal, caudal and anal fins. In particularly dark individuals, the basal portion of the pectoral fin is similarly dark but lacks the distinct black spot present in *P. bachus* and *P. palmata*. *Pseudophycis barbata* is easily separable from *P. breviuscula* by the more numerous scales (16–22 vs. 7–9) in a transverse row between the dorsal fin origin and lateral line.

As mentioned above under Remarks for *P. palmata*, McCoy's (1878: 29) treatment of *P. barbata*, the first published after Günther's original description, was largely based on specimens of *P. palmata,* but the accompanying illustration is of a large specimen of *P. barbata*. Although Ramsay's (1881) description of *Lotella grandis* is inadequate for a conclusive identification of the species, the lone type specimen (AMS I.696) is clearly *P. barbata*. Early taxonomic confusion resulted in Steindachner (1901: 509) reporting *P. barbata* from New Zealand as *L. grandis*, Norman (1937: 55) speculating that *P. barbata* (as *Physiculus barbatus*) may be identical with *P. bachus*, and Graham (1938: 399) and Habib (1975) treating it in New Zealand as *P. breviusculus*. The last stems from our assumption that *P. breviusculus* does not occur in the waters of the South Island based on specimens examined and reliable identification records.

Material examined. Types. Pseudophycis barbatus BMNH 1863.1.15.38 (394, holotype) Victoria, South Australia (fig. 7a); *Lotella grandis* AMS I.696 (503, holotype) Wollongong, New South Wales.

Other material. (38 specimens examined for meristic or morphometric values, 111–531 mm SL; see Appendix 2 for additional material in Australasian collections.) **Australia, *Victoria:*** CSIRO H 3791-01† (340) south of Gabo Island, 37° 43.30' S, 149° 55.20' E–37° 41.10' S, 149° 57.10' E, 116–107 m, A. Graham, 17 September 1994; CSIRO H 4500-01† (410) south of Cape Everard, 38° 07.81' S, 149° 30.87' E, 156 m, A. Williams and M. Lewis, 13 January 1997; NMV A2248 (5, 134–185) Portland Harbour, halfway along lee breakwater, adjacent to oil wharf, 38° 20.916' S, 141° 37.398' E, 7–12 m, R. Kuiter, R. Wilson and I. Head, 22 October 1981; NMV A2261-001 (4, 149–180) Portland Harbour, end of lee breakwater, 38° 21' S, 141° 36' E, 12 m, R. Kuiter, R. Wilson and I. Head, 21 October 1981; NMV A13046 (203) eastern Bass Strait, 110 km E of Paradise Beach, 38° 18.7' S, 148° 50.7' E, 201–208 m, M. Gomon, 7 August 1993. ***Tasmania:*** AMS I.20079-009 (90.1) south side of Rocky Cape, in National Park, 40° 51' S, 145° 31' E, 2–8 m, B.C. Russell, 8 December 1977; CSIRO H 7539-03† (185) south-east of Orford, rock point W of Triabunna woodchip mill, 42°

32.92' S, 147° 54.80' E, 3 m, P.L Last, W. White and J. Pogonoski, 01 April 2014. ***South Australia:*** CSIRO CA 3526 (410 mm SL) Great Australian Bight, 32° 11.8' S, 131° 22.4' E–32° 13.4' S, 131° 22.2' E, 60 m, 7 December 1981; CSIRO H 7949-13† (2, 47–70) Great Australian Bight, 33° 20.20' S, 130° 15.42' E–33° 20.20' S, 130° 16.26' E, 191–188 m, A. Graham, J. Pogonoski, M.F. Gomon and D.J. Bray, 15 December 2015. ***Western Australia:*** WAM P.26621.003 (135) Porpoise Bay, 32°00' S, 115°30' E, 1 m. **New Zealand, *North Island***: NMNZ P.01930 (514) Wellington, Ohau Point, Makara Coast, 41 14.00' S, 174 39.00' E, 18 m, J. Moreland, 10 June 1956; NMNZ P.014921 (2, 207–240) Three Kings Islands, west end of Great Island, 34° 8.5' S, 172° 9.1' E, 5–7 m, G.S. Hardy and A.L. Stewart, 28 November 1983; NMNZ P.037109† (518) Mahina Knoll, NW of White Island, Bay of Plenty, 37° 20.46' S, 177° 5.43' E, 303 m, NMNZ/MARS White Island field team, 22 March 2009; NMNZ P.037124† (450) east of north-east point; White Island, Bay of Plenty, 37° 30.96' S, 177° 13.54' E, 296 m, NMNZ/MARS White Island field team, 19 March 2009; NMNZ P.044103† (250) southeast of Club Rock; White Island, Bay of Plenty, 37° 32.35' S, 177° 11.92' E, 99 m, NMNZ/MARS White Island field team, 16 March 2009; NMNZ P.044272 (376) and NMNZ P.044273 (361) Three Kings Islands, northern edge of Three Kings Shelf; north off Princess Islands, 114 m, NMNZ/MARS Three Kings field team, 10 March 2010; NMNZ P.045835† (197) east off Parengarenga Harbour entrance, 34° 30.93' S, 173° 18.05' E, 176 m, RV Kaharoa, 4 August 2009; NMNZ P.046563 (339) Three Kings Islands, at anchor, Northwest Bay; Three Kings Island, 34 9.16' S, 172 8.06' E, 27 m, C.D Struthers, 6 March 2010; NMNZ P.052585 (339) Northland, off North Cape, 34° 16.47' S, 173° 0.80' E, 130–132 m, RV Tangaroa, 25 March 2011; NMNZ P.052745† (443) eastern side of Motkokako Island, Cape Brett, 35° 9.90' S, 174° 20.27' E, S. Tindale, 7 September 2011; NMNZ P.053551† (531) Kingfish Reef, Bay of Islands, 35° 11.20' S, 174° 15.40' E, 35 m, S. Tindale, 8 April 2012. ***South Island:*** NMNZ P.035978 (2, 234–266) West Coast, Open Bay Island, south end Popotai Islet, 43° 51.82' S, 168° 52.48' E, 14–19 m, NMNZ Jackson-Haast field team, 14 February 1999; NMNZ P.036535 (3, 186–256) West Coast, Open Bay Island, south end Popotai Islet, 43° 51.82' S, 168° 52.48' E, 14–19 m, NMNZ Jackson-Haast field team, 14 February 1999; NMNZ P.037525 (4, 111–148) West Coast, North of Murphy Beach, Whakapohai Rocks, 43° 42.27' S, 169° 14.33' E, 12–14 m, NMNZ Haast-Buller field team, 18 February 2000. NMNZ P.053753 (281) off Snares Islands, 47° 59.99' S, 166° 36.25' E, 160 m, NMNZ/MARS Auckland Island field team, 21 February 2012; NMNZ P.053754 (390) Stewart Island, North Arm, Port Pegasus, 47° 10.73' S, 167° 40.95' E, 38 m, NMNZ/MARS Auckland Island field team, 20 February 2012.

Pseudophycis breviuscula (Richardson 1846)

Common name: Bastard Red Cod (Australian Standard); northern bastard cod (New Zealand)

Figures 1, 3C, 5, 8; Tables 1–4

Lota breviuscula Richardson, 1846: 61, Pl. 38 (figs 1–2). Type locality: Bay of Islands, New Zealand. Holotype: BMNH 1855.9.19.1182.

Pseudophycis breviusculus. Günther, 1862: 350; Günther, 1863: 116; Hector in Hutton and Hector, 1872: 116, pl. 8; Hutton in Hutton and Hector, 1872: 47; Dambeck, 1879: 536, 547, 555; Hector, 1884: 55; Hector, 1886: 28; Sherrin, 1886: 304; Gill, 1893: 120 (list); Hutton, 1904: 48; Thomson, 1906: 551; Young, 1925: 370; Graham, 1938: 405; Graham, 1939b: 365; Ayling and Cox, 1982: 143, fig. (description).

Austrophycis megalops Ogilby, 1897: 91. Type locality: Maroubra Bay, New South Wales, Australia. Holotype: AMS I.3655.

Austrophycis megalops. McCulloch, 1927: 32 (list); McCulloch, 1929: 129 (list); Munro, 1938: 62, fig. 443 (description); Whitley, 1964: 40 (list); Paxton and Hanley in Paxton et al., 1989: 302 (list).

?*Pseudophycis breviusculus*. Graham, 1939: 399.

Physiculus (Pseudophycis) breviusculus. Graham 1956: 173, 174 fig.; Whitley, 1956: 403 (list); Svetovidov, 1967: 1686, 1689; Whitley, 1968: 40 (list).

Pseudophycis breviuscula. Paulin, 1983: 93 (description, taxonomy); Francis, 1988: 21; Paxton and Hanley in Paxton et al., 1989: 302 (list); Paul, 1986: 58; Paulin, 1988: 450, 451, 453; Paulin et al., 1989: 119 (key), 255 (list); Cohen in Cohen et al., 1990: 375 (taxonomy); Paulin and Roberts, 1992: 128, fig. 68a (description); Kuiter, 1993: 60 (description); Gomon in Gomon et al., 1994: 335 (description); Francis, 1996: 21; Paul, 2000: 58; Francis, 2001: 25; Hutchins, 2001: 23 (distribution); Sazonov, 2001: 293 (taxonomy of *A. megalops*); Paxton et al., 2006: 616 (list); Gomon in Gomon et al., 2008: 314 (description); Roberts et al. in Gordon et al., 2009: 532 (list); McMillan et al., 2011a: 161, 162; McMillan et al., 2011b: 94; Francis, 2012: 52; Struthers et al., in Roberts et al., 2016: 864, fig. 107.22 (description); Roberts et al., 2015: S164; Roberts et al., 2017: 81, Roberts et al., 2019: 90 (listed).

?*Austrophycis marginata* (nec Günther, 1878). Cohen in Cohen et al., 1990: 356 (taxonomy of *A. megalops*).

Diagnosis. First dorsal fin with 8–10 rays, second dorsal fin with 44–52 rays; anal fin with 49–56 rays; total vertebrae 42–45; nostrils adjacent to anterior margin of orbit, interval between nostril and orbital margin less than diameter of combined nostrils; posterior nostril with raised anterior border but without tubular flap posteriorly; gill rakers of outer arch moderately short, those near angle much shorter than opposing gill filaments; caudal peduncle short 28.8–33.4% HL; chin barbel of moderate length, 23.4–30.5% HL; scales above lateral line in oblique series from base of first dorsal fin ray 7–9; oblique rows of scales intersecting with lateral line 77–93; pyloric caeca 7–8; caudal fin rounded without angular corners, the middle rays equal to or longer than the rays above and below; no distinct dark blotch at base of pectoral fin; underside of head, body and anal fin tan to brown, anal fin with fine black distal margin. A small species reaching at least 151 mm SL.

Description. (Values for non-type specimens when different from type in parentheses; see Tables 2–4 for summary of selected meristic and comparative morphometric values.) First dorsal fin 9 (8–10, rarely 8), first ray often minute; second dorsal fin 46 (44–52, rarely less than 46); anal fin 50 (49–56); pectoral fin 21 (20–23); pelvic fin 4 (4–5); caudal fin 26 (26–32, rarely 26); gill rakers 3 (2–3) + 8 (7–8) = 9–12; lateral line pores not associated with individual scales; oblique scale rows intersecting with lateral line 93 (77–93); scales in oblique series above lateral line 7 (7–9), scales in oblique series below lateral line 23 (22–28, rarely 28); vertebrae 13 (11–14, rarely 11) + 31 (30–33) = 42–45, rarely 42; pyloric caeca 7–8.

Body of moderate depth, moderately compressed laterally (fig. 8), greatest depth at or just in advance of anal fin origin 22.8 (20.6–23.3)% SL, tapering gradually from second dorsal fin origin to posterior portion of fin and then more steeply to shallow caudal peduncle; caudal peduncle short, 4.8 (5.7–8.5)% SL, strongly compressed, depth subequal to orbital diameter. Distance between middle of anus and base of anal fin less than diameter of posterior nostril. Body cavity extending to above origin of anal fin.

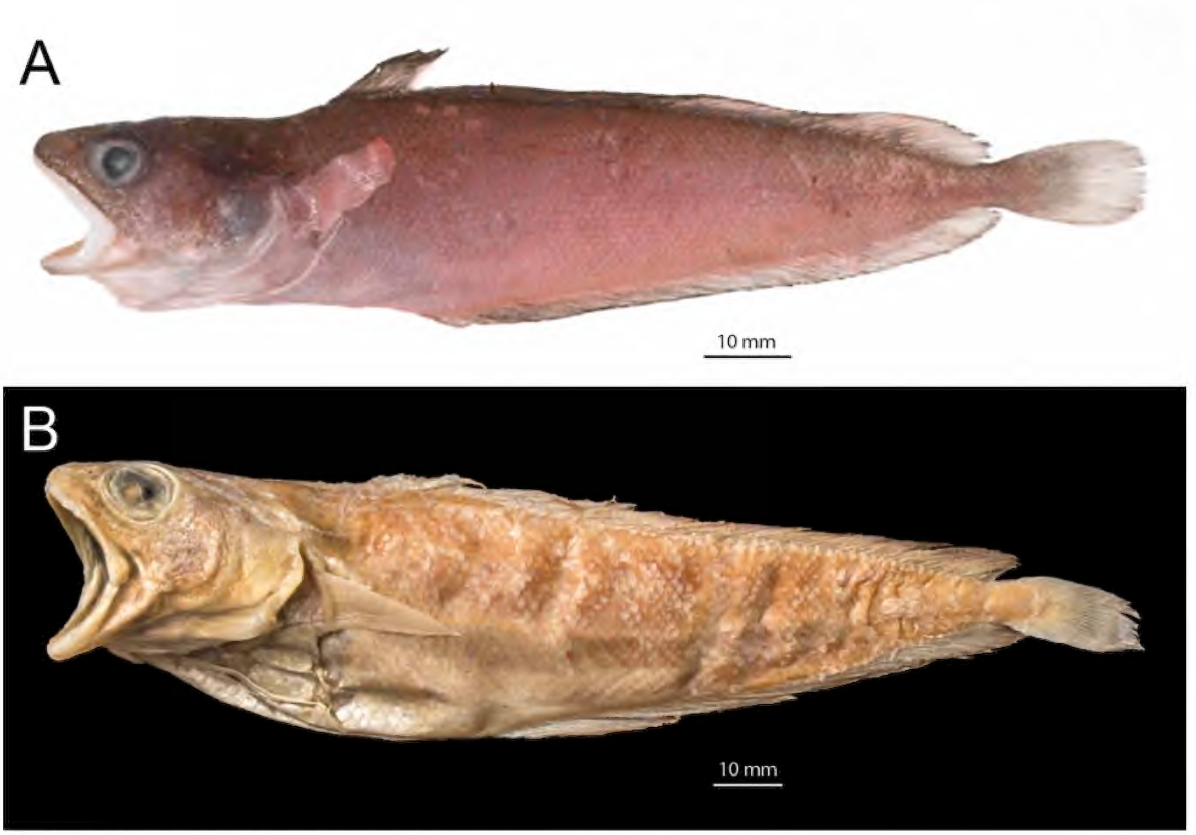

Figure 8. *Pseudophycis breviuscula*. A, CSIRO H 4384-01, 110 mm SL, Albany, Western Australia (photograph compliments CSIRO Marine Research); B, BMNH 1855.9.19.1182, holotype of *Lota breviuscula*, 152 mm SL, Bay of Islands, New Zealand (photograph © The Trustees of the Natural History Museum, London).

Head acute, moderately short, length 25.8 (23.4–26.0)% SL, its width 16.6 (12.4–17.9)% SL and depth 12.1 (10.8–15.2)% SL; snout moderately short 5.9 (5.1–7.0)% SL, not projecting in advance of upper jaw, rounded in dorsal view. Nostrils small, located on posterior half of snout just in front of eye, distance from nostrils to orbital margin less than diameter of combined nostrils; nostrils positioned above horizontal through centre of eye; diameter of posterior opening about 1.5 diameter of anterior, separated from it by raised skin flap; posterior opening without tubular flap encircling posterior margin. Interorbital of moderate width, slightly convex. Eye of moderate size, orbital diameter 27.4 (24.7–35.7)% HL, 0.91 (0.53–1.10) times in interorbital space, 3.72 (2.20–5.78) times suborbital distance, circular, upper edge of eye just below dorsal margin of head in lateral view, skin covering eye unpigmented. Postorbital moderately long, 1.09 (0.97–1.50) times length of upper jaw. Mouth large, terminal, upper jaw terminating just posterior to vertical through posterior margin of eye. Jaw teeth small, caniniform, slightly curved, depressible, band of up to four or five irregular rows in upper jaw with narrow hiatus at symphysis; band tapering near rear of jaw. Teeth of lower jaw similar in form to those of upper jaw; band of several rows with broader patch on either side of symphysis, tapering posteriorly; rows almost contiguous across symphysis. Vomerine teeth absent. Opercular bones strong; upper extremity of gill opening at horizontal through middle of eye; gill membranes continuous across isthmus. Gill rakers on outer arch club-shaped, moderately short, about 0.3–0.8 times length of opposing gill filaments at angle, 15–23 times in head, slightly denticulate. Chin barbel of moderate length, subconical 21.0 (19.6–30.5)% HL.

Moderately small cycloid scales covering all of head and body except for branchiostegal membranes, surface of maxilla and premaxilla, lower lip and distal parts of fins; very thick mucus covering obscuring scales and pores in freshly preserved material. Most head pores tiny, following main cephalic sensory canals; row of slightly raised pores extending from tip of snout posteriorly just above lower edge of suborbital; row of enlarged mandibular pores on underside of lower jaw. Lateral line comprising pores on tubes arising above upper end of gill opening, anterior end curved upwards slightly, then gradually descending to lateral midline below

posterior third of second dorsal fin, remaining on lateral midline posteriorly.

Membranes of first and second dorsal fins continuous at base; first dorsal originating distinctly behind vertical through pectoral fin base; anterior two-thirds of second dorsal of uniform height, 7th to 9th ray from posterior end of fin longest, its height about 1.2 times length of 2nd ray at anterior end of fin, last eight or so rays progressively shorter; rays of both dorsal fins mostly unbranched, only about last 14 or 15 rays, except last few, branched. Fleshy basal sheath on base of first dorsal and anterior portion of second dorsal fins not especially prominent with scales apparently confined to basal margin of fin; fin rays interconnected by membranes to tips; sheath more obvious on body below much of combined dorsal fin base, broadest anteriorly, narrowing posteriorly. Profile of anal fin similar to that of second dorsal fin, with comparable unbranched and branched rays. Fleshy sheath on and below anal fin similar to that of dorsal fins. Caudal fin rounded without distinct dorsoposterior and ventroposterior corners, posterior margin distinctly convex; all but anteriormost rays of similar length; base of fin covered by indistinct sheath (sheath demarcated from scales of caudal peduncle). Pectoral fin tip reaching past vertical through anal fin origin, seventh or eighth ray longest. Pelvic fin inserted anterior to vertical through posterior edge of preopercle; outer two rays longer than inner rays; second ray longest, 17.6 (16.6–21.6)% SL, two to four times length of subsequent ray, reaching vertical through first dorsal fin origin.

Fresh colour. (Based on images of non-type material; fig. 8B.) Medium brown to pale brown above, paler below with white chest and belly in smaller individuals, bronze in larger individuals; lateral line not distinctive. Underside of head and jaws brownish; ventral edge of suborbital darker brown; barbel white. Dorsal, anal and caudal fins very pale brown in smaller individuals, darker in large individuals; fins with distinct broad to narrow black margin distally, more diffuse in large individuals. Pectoral fin orange with very faint semi-circular brown blotch basally. Pelvic fin rays white with pink to orange hue.

Preserved colour. Head, body and fins pale dusky to dusky, chest and belly very pale, ventral edge of suborbital darker; distal edges of dorsal, caudal and anal fin with diffuse darker margins.

Etymology. The name *breviuscula* is Latin for "rather short", probably in reference to the relatively small maximum size of the species compared with others of the genus, although Richardson separated it from other New Zealand morids simply by fin counts.

Distribution. Endemic to coastal waters of Australia and New Zealand, from Perth, Western Australia (32° 01' S, 115° 30' E), to Tweed Heads, New South Wales (28° 14' S, 153° 50' E), including all of Tasmania and around the North Island of New Zealand (fig. 3C). A demersal reef-dwelling species at 0–273 m, although most often encountered at less than 100 m on rocky and boulder reefs (Struthers et al. in Roberts et al., 2016: 864).

Remarks. P. breviuscula is the smallest of the four species in the genus, reaching less than half the maximum length of its congeners. It also occurs in slightly warmer waters compared with the other three members of the genus, reaching well onto the northern New South Wales coast in eastern Australia and around New Zealand's North Island.

Paulin (1983: 94) provided a thorough synonymy of *P. breviuscula* from a New Zealand perspective but failed to mention *Austrophycis megalops* Ogilby, 1897, which was based on a specimen from New South Wales, Australia. This omission was possibly due to the widespread uncertainty about the identity of Waite's shrivelled 65 mm type specimen. Some authors regarded Ogilby's species as congeneric with Günther's (1878: 19) *A. marginatus* based on material from the south-eastern Pacific and others thought the two were likely to be conspecific (Cohen in Cohen et al., 1990: 356). Sazonov (2001: 343) reported that he had examined the type specimen and found it to be *P. breviuscula* relegating the name *A. megalops* to synonymy with that species.

Material examined. Types. Lota breviuscula BMNH 1855.9.19.1182 (152, holotype) Bay of Islands, New Zealand (fig. 8a); *Austrophycis megalops* AMS I.3655 (65, holotype) Maroubra Bay, New South Wales, Australia, 33° 57' S, 151° 16' E, T. Whitelegge, 1897 (after Sazonov, 2001: 343, holotype, not re-examined for this study).

Other material. (47 specimens examined for meristic or morphometric values, 70.2–139 mm SL; see Appendix 2 for additional material in Australasian collections.) **Australia,** ***Victoria:*** NMV A2261-002 (2, 106–111) Portland Harbour, end of lee breakwater, 38° 21' S, 141° 36' E, 12 m, R. Kuiter, R. Wilson and I. Head, 21 October 1981; NMV A8882 (2, 84.0–127) Bass Strait, 80 km south-east of Loch Sport, 38° 34.3' S, 148° 18.2' E, 86 m, Victorian Marine Sciences Laboratory, 6 June 1984. ***Tasmania:*** CSIRO H 7698-09† (66) Huon Commonwealth Marine Reserve, 43° 42.72' S, 147° 11.32' E–43° 42.97' S, 147° 10.35' E, 122 m, A. Graham and J. Pogonoski, 8 April 2015. ***Western Australia:*** WAM P.25342.004 (112) Cape Naturaliste, 33°32' S, 115°01' E, J. Scott, 16 February 1964; WAM P.25343.017 (2, 108–119) Fremantle, 32°02' S, 115°40' E, L.M. Marsh et al, 24 June 1975; WAM P.26616.005 (125) Point Clune, 32°00' S, 115°30' E, 8 m, J.B. Hutchins et al, 29 March 1979; WAM P.28297.006 (5, 59.4–139) Lucky Bay, 34°08' S, 122°15' E, 8–10 m, J.B. Hutchins, 13 April 1984; WAM P.28300.005 (5, 63.8–131) Lucky Bay, 34°05' S, 122°15' E, 11–12 m, J.B. Hutchins et al, 16 April 1984. **New Zealand,** ***North Island:*** NMNZ P.028044 (9, 82–127) Matatuahu Point, Tawharanui Peninsula, Hauraki Gulf, 36° 23' S, 174° 49' E, 0–5 m, A.L Stewart and C.D. Paulin, 8 April 1992; NMNZ P.028118 (7, 62–119) Onepoto Bay, Hicks Bay, East Cape, 37° 35.25' S, 178° 18.00' E, 0–3 m, NMNZ East Cape 1992 field team, 4 May 1992; NMNZ P.029805 (3, 55–135) Waihau Bay, Bay of Plenty, 37° 36.8' S, 177° 54.6' E, 4–6 m, NMNZ East Cape 1993 field team, 27 January 1993; NMNZ P.030036 (4, 103–135) inside of Tuamotu Island, Gisborne Harbour, 38° 42.2' S, 178° 2.4' E, 4–7 m, NMNZ East Cape 1993 field team, 21 January 1993; NMNZ P.046263 (103) north of Tom Bowling Bay; North Cape, 34° 22.56' S, 172° 55.28' E, 61–72 m, RV Tangaroa, 14 July 2009; NMNZ P.046285† (2, 72.2–81.4) east of Purerua Peninsula, Bay of Islands, 35° 6.36' S, 174° 17.10' E, 119–121 m, RV Tangaroa, 7 July 2009; NMNZ P.048310 (70.4) western end of Omapere wharf, 35° 32.05' S, 173° 23.14' E, 4 m, NMNZ & AIM Northland 2011 field team, 13 February 2011; NMNZ P.048311 (70.5) western end of Omapere wharf, 35° 32.05' S, 173° 23.14' E, 4 m, NMNZ & AIM Northland 2011 field team, 13 February 2011; NMNZ P.048312 (82.6) western end of Omapere wharf, 35° 32.05' S, 173° 23.14' E, 4 m, NMNZ & AIM Northland 2011 field team, 13 February 2011; NMNZ P.048380 (124), NMNZ P.048381 (96.8) and NMNZ P.048382 (3, 59.9–101) reef inside southern

headland of Hokianga Harbour, 35° 32.01' S, 173° 22.10' E, 5–8 m, WCN 11/09, NMNZ & AIM Northland 2011 field team, 15 February 2011; NMNZ P.049600 (84.8) and NMNZ P.049703 (93) Tauroa Point, Ahipara, 35° 10.48' S, 173° 2.73' E, 21 m, WCN 11/35, NMNZ & AIM Northland 2011 field team, 22 February 2011; NMNZ P.049708 (100) Tauroa Point, Ahipara, 35° 9.96' S, 173° 3.12' E, 14 m, NMNZ & AIM Northland 2011 field team, 22 February 2011; NMNZ P.051786 (119) Tauroa Point, Ahipara, 35° 10.48' S, 173° 2.73' E, 21 m, NMNZ & AIM Northland 2011 field team, 22 February 2011; NMNZ P.057218† (78.5) and NMNZ P.052719† (82.3) Ranfurly Bank, 37° 32.78' S, 178° 53.42' E, 68–70 m, RV Tangaroa, 30 May 2011.

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Appendix 1. CO1 sequences and source information for *Pseudophycis* spp featuring in Figure 1.

Species	Source Institution	Voucher Reg No./ Sample ID No.	Country	Collection Locality	BOLD Sequence ID	GenBank accession
A. punctatus	NMNZ	P.045573	New Zealand	South Island, west coast	FNZC105-09	MN200065
A. punctatus	NMNZ	P.045574	New Zealand	South Island, west coast	FNZC106-09	MN200089
A. punctatus	NMNZ	P.045575	New Zealand	South Island, west coast	FNZC107-09	MN200090
A. punctatus	NMNZ	P.045576	New Zealand	South Island, west coast	FNZC108-09	MN200094
A. punctatus	NMNZ	P.045577	New Zealand	South Island, west coast	FNZC109-09	MN200092
A. punctatus	NIWA	no voucher PCO1	New Zealand	South Island, west coast	FNZA333-07	MN200088
A. punctatus	NIWA	no voucher PCO2	New Zealand	South Island, west coast	FNZA334-07	MN200093
P. bachus	NIWA	no voucher RCO1	New Zealand	Campbell Island	FNZ949-07	MN200031
P. bachus	NIWA	no voucher RCO4	New Zealand	Campbell Island	FNZ950-07	MN200023
P. bachus	NIWA	no voucher RCO5	New Zealand	Auckland Islands	FNZA351-07	MN200039
P. bachus	NIWA	no voucher RCO6	New Zealand	Auckland Islands	FNZA352-07	MN200027
P. bachus	NIWA	no voucher RCO7	New Zealand	no data	FNZA388-08	MN200026
P. bachus	NIWA	no voucher RCO8	New Zealand	no data	FNZA389-08	MN200030
P. bachus	NIWA	no voucher RCO9	New Zealand	no data	FNZA390-08	MN200028
P. bachus	NMNZ	P.044338	New Zealand	South Island, south of Timaru	FNZA555-08	MN200037
P. bachus	NMNZ	P.044339	New Zealand	South Island, south of Timaru	FNZA556-08	MN200029
P. bachus	NMNZ	P.044348	New Zealand	Chatham Rise	FNZA557-08	MN200062
P. bachus	NMNZ	P.044349	New Zealand	Chatham Rise	FNZA558-08	MN200024
P. bachus	NMNZ	P.044350	New Zealand	Chatham Rise	FNZA559-08	MN200040
P. bachus	NMNZ	P.053748	New Zealand	Stewart Island, Port Pegasus		MN200063
P. bachus	NMNZ	P.053749	New Zealand	Stewart Island, Port Pegasus		MN200069
P. bachus	NMNZ	P.053750	New Zealand	Stewart Island, Port Pegasus		MN200076
P. bachus	NMNZ	P.053751	New Zealand	Stewart Island, Port Pegasus		MN200075
P. bachus	NMNZ	P.053752	New Zealand	Stewart Island, Port Pegasus		MN200035
P. bachus	NMNZ	P.054828 (Neotype)	New Zealand	North Island, Whanganui Bar		MN200038
P. barbata	CSIRO	H 3791-01	Australia	VIC, Gabo Island	FOAD135-05	MN200087
P. barbata	CSIRO	H 4500-01	Australia	VIC, Cape Everard	FOAD141-05	MN200080
P. barbata	CSIRO	H 7539-03	Australia	TAS, Orford	FOAO050-14	MN200085
P. barbata	CSIRO	H 7904-03	Australia	SA, Great Bight	FOAP009-16	MN200086
P. barbata	CSIRO	H 7949-13	Australia	SA, Great Bight	FOAP215-16	MN200079
P. barbata	CSIRO	no voucher	Australia	NSW, Cape Howe	FOAD137-05	MN200083
P. barbata	CSIRO	no voucher	Australia	NSW, Diaster Bay	FOAD138-05	MN200078
P. barbata	CSIRO	no voucher	Australia	NSW, Diaster Bay	FOAD139-05	MN200081
P. barbata	CSIRO	no voucher	Australia	NSW, Diaster Bay	FOAD140-05	MN200082
P. barbata	CSIRO	no voucher GT 10004	Australia	SA, Great Bight	FOAP335-17	MN200084
P. barbata	NIWA	no voucher SBR1	New Zealand	no data	FNZA383-08	MN200073
P. barbata	NIWA	no voucher SBR2	New Zealand	no data	FNZA384-08	MN200072
P. barbata	NIWA	no voucher SBR3	New Zealand	no data	FNZA385-08	MN200074
P. barbata	NIWA	no voucher SBR4	New Zealand	no data	FNZA386-08	MN200070
P. barbata	NIWA	no voucher SBR5	New Zealand	no data	FNZA387-08	MN200066
P. barbata	NIWA	no voucher SBR6	New Zealand	North Island, Ngawi	FNZA608-08	MN200036
P. barbata	NIWA	no voucher SBR7	New Zealand	North Island, Ngawi	FNZA609-08	MN200068
P. barbata	NMNZ	P.037109	New Zealand	North Island, White Island	FNZC188-09	MN200091
P. barbata	NMNZ	P.037124	New Zealand	North Island, White Island	FNZC189-09	MN200077
P. barbata	NMNZ	P.044103	New Zealand	North Island, White Island	FNZC280-09	MN200071
P. barbata	NMNZ	P.045835	New Zealand	North Island, East coast	FNZC252-09	MN200067
P. barbata	NMNZ	P.052745	New Zealand	North Island, Cape Brett		MN200025
P. barbata	NMNZ	P.053551	New Zealand	North Island, Bay of Islands		MN200033
P. breviuscula	CSIRO	H 6838-08	Australia	NSW, Broken Bay	FOAK632-10	MN200059

Species	Source Institution	Voucher Reg No./ Sample ID No.	Country	Collection Locality	BOLD Sequence ID	GenBank accession
P. breviuscula	CSIRO	H 6838-08/2	Australia	NSW, Broken Bay	FOAK604-10	MN200053
P. breviuscula	CSIRO	H 6845-01/1	Australia	NSW, Broken Bay	FOAK626-10	MN200054
P. breviuscula	CSIRO	H 6845-01/2	Australia	NSW, Broken Bay	FOAK612-10	MN200055
P. breviuscula	CSIRO	H 6845-01/3	Australia	NSW, Broken Bay	FOAK610-10	MN200060
P. breviuscula	CSIRO	H 6980-04	Australia	TAS, east coast	FOAK246-10	MN200057
P. breviuscula	CSIRO	H 6991-01	Australia	TAS, east coast	FOAK247-10	MN200056
P. breviuscula	CSIRO	H 7698-09	Australia	TAS, northeast	FOAO611-15	MN200064
P. breviuscula	NMNZ	P.046285	New Zealand	North Island, Bay of Islands	FNZC272-09	MN200058
P. breviuscula	NMNZ	P.046285-1	New Zealand	North Island, Bay of Islands	FNZC271-09	MN200061
P. breviuscula	NMNZ	P.052718	New Zealand	North Island, Ranfurly Bank		MN200032
P. breviuscula	NMNZ	P.052719	New Zealand	North Island, Ranfurly Bank		MN200034
P. palmata	NMV	A 26125-002	Australia	VIC, Port Phillip Bay	FMVIC234-08	MN200052
P. palmata	NMV	A 31132-001	Australia	TAS, east coast	FOAO533-15	MN200043
P. palmata	CSIRO	H 4229-01	Australia	TAS, southeast	FOAD136-05	MN200041
P. palmata	CSIRO	H 7366-01	Australia	TAS, North Bruny Island		MN200048
P. palmata	CSIRO	H 7716-01	Australia	TAS, Munro Bight	FOAO599-15	MN200047
P. palmata	CSIRO	H 7717-01	Australia	TAS, Hinsby Beach	FOAO600-15	MN200051
P. palmata	CSIRO	no voucher BW-1692	Australia	VIC, Bass Strait	FOAD132-05	MN200050
P. palmata	CSIRO	no voucher BW-1693	Australia	VIC, Bass Strait	FOAD133-05	MN200044
P. palmata	CSIRO	no voucher BW-1694	Australia	VIC, Bass Strait	FOAD134-05	MN200042
P. palmata	CSIRO	no voucher GT 7974	Australia	TAS, east coast	FOAO596-15	MN200045
P. palmata	CSIRO	no voucher GT 7975	Australia	TAS, east coast	FOAO597-15	MN200046
P. palmata	CSIRO	no voucher GT 7976	Australia	TAS, southeast	FOAO598-15	MN200049

Appendix 2. Specimens registered in Australasian collections not used for compiling morphological data. Not all specimens listed were examined in the course of the study.

Physiculus palmata

(78 specimens, 30–410 mm SL.) **Australia**: AMS I.7534 (310) no locality, 1905. ***New South Wales:*** AMS I.15024 (420) Merimbula, 36°53' S, 149°56' E, 1908; AMS I.34458-001 (87) one third of way to Tollgate Island from Three Islet Reef Batemans Bay, 35°44' S, 150°15.5' E, 100 m, 23–24 November 1988; AMS I.34461-001 (190) Lookout Point, Twofold Bay, 37°4.5' S, 149°55' E, 50 m, 26–27 November 1988; AMS I.34566-001 (225) Batemans Bay west end of Long Beach, 35°42' S, 150°13' E, 50 m, 23–24 November 1988; AMS I.34568-001 (128) North Head Beach, Batemans Bay, 35°43' S, 150°16' E, 50 m, 23–24 November 1988; CSIRO H3537-01 (5, 54–97) south of Disaster Bay, 37°24.2' S, 149°58.4' E–37°22.9' S, 149°58.7' E, 42–44 m, 13 August 1993. ***Victoria:*** NMV A639 (221) off Phillip Island, 38°39' S, 145°19.8' E, 07 August 1979; NMV A836 (2, 104–138) Port Phillip Bay, 38°06' S, 144°52.8' E, 1970; NMV A837 (2, 129–133) Port Phillip Bay, 38°06' S, 144°52.8' E, 1971; NMV A838 (2, 134–146) Port Phillip Bay, 3.2 km (2 miles) Port Phillip Bay, west of Sandringham, 37°57' S, 144°57' E, 30 March 1971; NMV A839 (250) Port Phillip Bay, 38°06' S, 144°52.8' E, 25 July 1927; NMV A841 (2, 245–250) Port Phillip Bay, Hobsons Bay, 37°52.2' S, 144°55.8' E, September 1867; NMV A846 (2, 190–207) Port Phillip Bay, Hobsons Bay, 37°52.2' S, 144°55.8' E, September 1867; NMV A848 (315) no data, old collection; NMV A2285 (51.4) central Bass Strait, 38 km southwest of Cape Paterson, 38°55.5' S, 145°17' E, 70 m, 12 November 1981; NMV A2667 (51.8) Eastern Bass Strait, 8 km south of South East Point, Wilsons Promontory, 39°12.9' S, 146°27.3' E, 65 m, 18 November 1981; NMV A10580 (242) Western Port, 5 km north of Cowes, 38°26.1' S, 145°15.3' E, 20 m, 22 October 1986; NMV A20816 (2, 201–210) no data, old collection, August 1864; NMV A26125-002 (61.0) Port Phillip Bay, central part of bay, east of St Leonards, 38°12.8' S, 144°50' E, 24 m, 12 December 1996; NMV A23366-002 (401) no data, old collection; NMV A31156-001 (237) Port Phillip Bay, Hobsons Bay, 37.87°S, 144.93°E; NMV A31157-001 (223) same collection data as NMV A31156-001. ***Tasmania:*** AMS IB.1192 (142) d'Entecasteaux Channel, Simpsons Bay, 43°17' S, 147°18' E, 7 July 1942; AMS I.10287 (140), Oyster Bay, 42°40' S, 148°03' E, 1909; AMS I.14182 (300) Port Arthur, 43°09' S, 147°51' E, 13 April 1917; AMS I.14183 (248) Port Arthur, 43°09' S, 147°51' E, 13 April 1917; AMS I.6243 (62) NW coast: Ulverston, 41°10' S, 146°11' E, 1903; AMS I.6275 (340) Tamar River Heads, 41°20' S, 147°02' E, 1903; AMS I.6276 (245) Tasmania, Tamar River Heads, 41°20' S, 147°02' E, 1903; AMS I.9259 (252) Port Arthur, 43°09' S, 147°51' E, 1908; AMS I.9989 (177) Bass Strait, east of Flinders Island, 40°01' S, 148°42' E, 1909; AMS I.9990 (195) Bass Strait, east of Flinders Island, 40°01' S, 148°42' E, 1909; NMV A1218-003 (2, 297–299) Central Bass Strait, 20 km north-northeast of North Point, 40°31.8' S, 145°22.8' E, 44 m, BSS 116 T, M.F. Gomon, G.C.B. Poore, and P. Forsyth, 4 November 1980; NMV A1289 (294) central Bass Strait, 23 km east of Cape Rochon, Three Hummock Island, 40°22.2' S, 145°17' E, 40 m, 3 November 1980; NMV A1381 (38.5) central Bass Strait, 6 km northeast of Stanley, 40°48.8' S, 145°22' E, 22 m, 4 November 1980; NMV A1479 (67.2) central Bass Strait, 32 km west-southwest of Settlement Point, Flinders Island, 40°9.95' S, 147°31.8' E, 51–52 m, 6 February 1981; NMV A1535 (8, 163–220) central Bass Strait, 32 km northwest of Devonport, 40°56' S, 146°5.4' E, 68–64 m, 4 February 1981; NMV A9776 (272) near Marlo Reef, 37°48' S, 148°31.8' E, 1991; NMV A9777 (276) Marlo Reef, 37°48' S, 148°31.8' E, 1991; NMV A20556 (202) Bass Strait, east coast of Flinders Island, 40° S, 148°20' E, 73 m, 16 June 1909; NMV A21590 (4, 150–182) Bass Strait, east of Flinders Island, 40°S, 148°33' E, 1909; WAM P.27554.001 (186) Spring Bay, 42°32' S, 147°55' E, 1–8 m; ***South Australia:*** SAMA F 2777 (1) Gulf St Vincent, 34°11' S, 138°9' E, 14 July 1953; SAMA F4624 (8) Robe, 37°10' S, 139°45' E, 9 September 1979; SAMA F7172 (1) Spencer Gulf, Port Lincoln, 34°44' S, 135°52' E, 1992; SAMA F10581 (1), Robe, bay near river mouth, 16 March 2003; SAMA F10855 (1) Investigator Strait, 35°24'28" S, 137°54'40" E, 16 December 2006; SAMA F10900 (1) Investigator Strait, 35°19' 09" S, 137°46' 05" E, 15 December 2006; SAMA F11864 (1) Great Australian Bight, Coles Point, 34°22'06" S, 135°21'09" E, 21 March 2003; SAMA F12755 (1) Victor Harbour, 35°33' S, 138°37' E, 14 September 2003.

Pseudophycis bachus

(416 specimens, 21–573 mm SL.) **New Zealand**, ***North Island:*** NMNZ P.001129 (373) Wellington, Ngauranga, Wellington Harbour, 41°15' S, 174°50' E, 3 August 1952; NMNZ P.001809 (174) North Auckland, off Kaipara Bar, 36°24' S, 174°9.5' E, 183 m, August 1955; NMNZ P.002271 (227) Wellington, Wellington Harbour, off Petone, 41°14.0' S, 174°52.5' E, 13–18 m, 22 August 1957; NMNZ P.002372 (neurocranium) Wellington, York Bay, Wellington Harbour, 41°15.9' S, 174°54.2' E, 10–11 m, 31 May 1953; NMNZ P.002440 (2, otoliths) Wellington, Wellington Harbour, 41°16.5' S, 174°51.0' E, 1953; NMNZ P.003011 (otoliths and skeleton) Wellington, Paraparaumu Beach, 40°53' S, 174°56' E, 8 January 1961; NMNZ P.004788 (11, 71–128) Wellington, Palliser Bay, 41°26.3' S, 175°3.0' E, 64–82 m, 15 February 1968; NMNZ P.006562 (10, 73–99) north of Kapiti Island, off Foxton, 40°30.5' S, 174°53.0' E, 101 m, 1 March 1976; NMNZ P.006802 (2, 212–243) Bay of Plenty, 8 km north of Mayor Island, 37°12' S, 176°15' E, 366 m, 28 September 1962; NMNZ P.007357 (otoliths) Wellington, Te Mimi, south end of Kapiti Island, 40°52.35' S, 174°54.60' E, 3 m, 22 August 1977; NMNZ P.007441 (otoliths) Wellington, 11 January 1978; NMNZ P.008363 (3, 90–94) South Auckland, east-northeast of Tolaga Bay, 38°15.2' S, 178°38.6' E, 139 m, 16 January 1979; NMNZ P.009415 (84) Gisborne, Matakaoa, East Cape, 37°34' S, 178°20' E, 15 m, 26 June 1988; NMNZ P.009823 (3, 79–112) Taranaki, west-northwest of Cape Egmont, 38°48.8' S, 173°29.6' E, 146 m, 9 January 1981; NMNZ P.010543 (315) Bay of Plenty, north of Mayor Island/east of Slipper Island,

37°4.95' S, 176°12.70' E, 315–352 m, 18 April 1981; NMNZ P.014082 (2, 107–109) Wellington, off Castle Point, 40°56.25' S, 176°22.80' E, 115–140 m, 17 April 1978; NMNZ P.016708 (10, 32–68) Wellington, east of Cape Campbell, 41°44.15' S, 174°27.65' E, 47 m, 15 December 1978; NMNZ P.017108 (293) Taranaki, Seal Rocks, Sugar Loaf Islands, New Plymouth, 39°3.25' S, 174°0.20' E, 30 m, 24 March 1985; NMNZ P.017508 (2, 96–100) Wellington, Hikurangi Trench, 40°54.8' S, 176°25.4' E, 140 m, 17 April 1976; NMNZ P.017509 (102) Wellington, Hikurangi Trench, 40°57.7' S, 176°20.2' E, 115 m, 17 April 1976; NMNZ P.018714 (2, 52–57) Manawatu, southwest of Whanganui, 40°22.65' S, 174°22.80' E, 62–80 m, 17 July 1985; NMNZ P.019115 (57) Gisborne, east of Tolaga Bay, 38°23.05' S, 178°26.65' E, 30 m, 11 January 1980; NMNZ P.019331 (50) Hawke's Bay, Cape Kidnappers, 39°39' S, 177°10' E, 36 m, 19 October 1969; NMNZ P.023430 (230) Gisborne, Matakaoa, East Cape, 37°34' S, 178°20' E, 15 m, 26 June 1988; NMNZ P.029685 (5, 310–360) off Mohaka, 39°15' S, 177°20' E, 17 November 1992. ***South Island:*** AMS I.14733 (440) Portobello, Otago Harbour, 45°51' S, 170°39' E, 13 December 1918; AMS I.14734 (550) Otago, Blueskin Bay, 45°44' S, 170°35' E, 29 November 1918; NMNZ P.001753 (148) Otago, edge of Karitane Canyon, northeast of Tairoa Head, 45°38.5' S, 171°2.0' E, 220 m, 14 August 1955; NMNZ P.006548 (2, 90–109) Marlborough, Western Cook Strait; ca 14 km northeast of Stephens Island, 40°33' S, 174°7' E, 130–132 m, 4 March 1976; NMNZ P.006704 (278) Canterbury, northeast Mernoo Bank, Chatham Rise, 43°10.5' S, 174°58.5' E, 298–422 m, 23 June 1975; NMNZ P.007180 (305) Snares Islands, west side of western chain, Snares Island, 48°3' S, 166°30' E, 120 m, 4 December 1976; NMNZ P.007349 (200) Marlborough, Kaikoura area, 41°20' S, 174°9' E; NMNZ P.007442 (otoliths) Marlborough, 'Run Under Point'; Cook Strait between Port Underwood and Tory Channel, 41°18.25' S, 174°14.55' E, 19 January 1978; NMNZ P.007457 (505) Canterbury, Western Chatham Rise, off Mernoo Bank, 43°16.45' S, 174°55.50' E, 220 m, 11 December 1977; NMNZ P.007730 (12, 31–123) Marlborough, Cloudy Bay, 41°26.1' S, 174°15.9' E, 59–64 m, 28 January 1979; NMNZ P.008107 (79) Nelson, 6.4 km northwest of Farewell Spit, 40°27.0' S, 172°48.5' E, 70 m, 10 March 1976; NMNZ P.008355 (185) Southland, Crooked Arm, Fiordland, 45°25' S, 166°58' E, 16 m, 7 January 1977; NMNZ P.008356 (14, 67–105) Marlborough, Cloudy Bay, 41°26.35' S, 174°9.70' E, 27–28 m, 28 January 1979; NMNZ P.008365 (18, 60–118) Marlborough, Cloudy Bay, 41°26.35' S, 174°9.70' E, 27–28 m, 28 January 1979; NMNZ P.009282 (5, 228–360) Canterbury, Western Chatham Rise, off Mernoo Bank, 43°16.45' S, 174°55.50' E, 220 m, 11 December 1977; NMNZ P.009283 (7, 170–213) Canterbury, Western Chatham Rise, off Mernoo Bank, 43°16.45' S, 174°55.50' E, 220 m, 11 December 1977; NMNZ P.010598 (2, 168–170) Otago, off Oamaru, 45°5' S, 170°59' E, 46 m, July 1962; NMNZ P.010647 (115) Otago, Cape Wanbrow, off Oamaru, 45°7' S, 171°3' E, 100–101 m, June 1963; NMNZ P.010703 (65) Otago, Oamaru, 45°7' S, 174°22' E, 73 m, March 1973; NMNZ P.012069 (14, 57–75) Marlborough, Mernoo Bank, 43°6.1' S, 175°20.5' E, 153 m, 12 January 1979; NMNZ P.012088 (2, 65–80) Marlborough, Cloudy Bay, 41°26.35' S, 174°9.70' E, 27–28 m, 28 January 1979; NMNZ P.013119 (490) Snares Islands, Puysegur Trench, 46°49.15' S, 165°50.50' E, 459–515 m, October 1982; NMNZ P.016344 (272), Snares Islands, off North Promontory, 48°0' S, 166°36' E, 110 m, 5 December 1984; NMNZ P.017527 (2, 34–35) Stewart Island, Foveaux Strait, 46°30' S, 167°30' E, May 1976; NMNZ P.017876 (12, 58–80) Nelson, north of Cape Farewell, 40°4.65' S, 172°57.09' E, 102 m, 14 December 1978; NMNZ P.017879 (2, 36–60) Canterbury, northern Canterbury Bight, off Waiau River mouth, 42°36.8' S, 173°40.4' E, 81 m, 16 December 1978; NMNZ P.017884 (80) Nelson, north of Cape Farewell, 40°8.75' S, 173°11.15' E, 90 m, 14 December 1978; NMNZ P.017885 (5, 38–46) Canterbury, northern Canterbury Bight, off Kaikoura Peninsula, 42°39.30' S, 173°35.95' E, 130 m, 16 December 1978; NMNZ P.017891 (12, 28–40) Marlborough, off Cape Campbell, 41°42.1' S, 174°25.5' E, 60 m, 15 December 1978; NMNZ P.017892 (15, 33–64) Canterbury, northern Canterbury Bight, off Kaikoura Peninsula, 42°38.15' S, 173°39.75' E, 91 m, 16 December 1978; NMNZ P.017893 (15, 21–46) Marlborough, Cook Strait, east of Cape Campbell, 41°46.8' S, 174°28.6' E, 18 m, 15 December 1978; NMNZ P.018854 (48) Marlborough, east of Flaxbourne Depression, 41°59.9' S, 174°26.9' E, 100 m, 19 January 1982; NMNZ P.018865 (45) Marlborough, east of Flaxbourne Depression, 41°59.50' S, 174°30.55' E, 100 m, 19 January 1982; NMNZ P.018878 (69, 26–75) Canterbury, Canterbury Bight/southeast of Timaru, 44°43.4' S, 171°54.7' E, 95 m, 16 January 1982; NMNZ P.019322 (2, 45) Westland, northwest of Hokitika, 42°34.18' S, 170°15.19' E, 204 m, 10 December 1978; NMNZ P.019509 (99, 29–55) Canterbury, northeast of Clarence River mouth/central Campbell Bank, 42°6.00' S, 174°6.95' E, 84–86 m, 24 November 1982; NMNZ P.019831 (500) Southland, North Port, Fiordland, 45°59' S, 166°34' E, 27 m, 8 May 1986; NMNZ P.019949 (205) Southland, 30 Fathom Point, Fiordland, 45°43.3' S, 166°30.3' E, 36–37 m, 13 May 1986; NMNZ P.020802 (110) East coast South Island, 1982; NMNZ P.020806 (2, 72–76) East coast South Island, 1982; NMNZ P.025063 (3, 88–137) Otago, off Tairoa Head, Otago Peninsula, 45°45' S, 170°45' E, 1990; NMNZ P.025077 (3, 96–135) Otago, off Otago Peninsula, 45°36.55' S, 170°51.88' E, 41–59 m, 10 May 1990; NMNZ P.025093 (8, 76–116) Otago, off Otago Peninsula, 45°41.85' S, 170°58.72' E, 97–100 m, 10 May 1990; NMNZ P.025186 (90) Otago, Blueskin Bay, Otago Peninsula, 45°43.28' S, 170°40.33' E, 20–22 m, 9 May 1990; NMNZ P.025782 (2, 443–480) Canterbury, Pegasus Canyon, 43°23.78' S, 173°40.50' E, 113–109 m, 1 June 1990; NMNZ P.030708 (7, 87–120) Snares Islands, Southern Snares Shelf, 48°30.75' S, 166°58.50' E, 134–136 m, 1 April 1993; NMNZ P.032382 (420) Southland, Waterfall mooring, head of Bligh Sound, Fiordland, 44°50' S, 166°32' E, 8–10 m, 21 March 1995; NMNZ P.032398 (3, 395–410) Southland, mooring at Precipice Cove, Bradshaw Sound, Fiordland, 45°15' S, 167°10' E, 20 m, 28 March 1995; NMNZ P.036007 (2, 266–300) Westland, outer Frog Rock, 43°58.52' S, 168°33.48' E, 14–20 m, 11 February 1999; NMNZ P.036769 (2, 120–130) Canterbury, southwest of Timaru, 44°35.71' S, 171°12.55' E, 18–19 m, 20 December 1998; NMNZ P.045793 (104, C&S)

Marlborough, Cloudy Bay, 41°26.1' S, 174°15.9' E, 59–64 m, 28 January 1979. ***Bounty Islands:*** NMNZ P.006643 (573) Bounty Platform, southeast of Islands, 48°7.25' S, 179°16.25' E, 230–238 m, 18 November 1975. ***Auckland Islands:*** NMNZ P.007136 (264) northwest Auckland Islands/ Campbell Plateau, 50°10.35' S, 167°43.10' E, 120 m, 21 January 1977. ***Chatham Rise:*** NMNZ P.008357 (2, 78–79), Chatham Rise, Mernoo Bank, 43°36' S, 175°31' E, 375 m, 12 February 1954; NMNZ P.008358 (66) Mernoo Bank, Chatham Rise, 42°59.4' S, 175°30.5' E, 112 m, 23 January 1954; NMNZ P.009414 (2, 94–188) east of Chatham Islands, 43°30.95' S, 176°9.25'W, 176–205 m, 22 May 1987; NMNZ P.020910 (4, 100–125) Subantarctic Slope, 43°39.95' S, 175°51.40'W, 220–246 m, 28 May 1987; NMNZ P.020922 (270) northeast of Chatham Islands, 43°33.6' S, 176°0.5'W, 228–234 m, 26 May 1987; NMNZ P.020952 (273) east of Chatham Islands, 43°30.95' S, 176°9.25'W, 176–205 m, 22 May 1987; NMNZ P.020989 (2, 127–129) east of Chatham Islands, 43°39.15' S, 175°52.10'W, 216–244 m, 24 May 1987; NMNZ P.035283 (142) Urry Bank, Chatham Rise, 44°9.0' S, 176°6.5' E, 126 m, October 1979. ***Campbell Island:*** NMNZ P.009284 (390) Campbell Island Rise, northeast of Island, 51°51' S, 169°40' E, 250–271 m, 10 April 1982; NMNZ P.012110 (530), Campbell Island Rise, northeast of Island, 51°51' S, 169°40' E, 250–271 m, 10 April 1982.

Pseudophycis barbata

(211+ specimens, 26–620 mm SL.) **Australia:** AMS IB.7565 (465) no locality, 1966. ***New South Wales:*** AMS I.16970-014 (176) Boydtown, Nullica Bay, 37°6' S, 149°53' E, 13 March 1972; AMS I.19833-003 (5, 48–60) east of Ulladulla, 35°20' S, 150°51' E, 128 m, 14 May 1974; AMS I.25974-003 (91) Eden, eastern Bass Strait, 37°5' S, 149°55' E, 18–46 m, 26 November 1984; AMS I.27359-008 (270) Quarantine Beach inside North Head, 33°49' S, 151°18' E, 6 April 1967; AMS I.27359-009 (4, 105–180) Quarantine Beach inside North Head, 33°49' S, 151°18' E, 6 April 1967; AMS I.28908-001 (305) east of Shoalhaven Bight, 34°53' S, 151°06' E, 18 April 1985; AMS I.34570-002 (140) east of Lookout Point Twofold Bay, 37°46' S, 149°55' E, 26–27 November 1988; AMS I.34854-003 (115) off Newcastle, 33°2' S, 151°58 E, 117–121 m, 24 March 1993; AMS IB.8192 (514) Eden, 37°4' S, 149°55' E, 9 June 1968; CSIRO A 1117 (72 mm TL) between Cronulla and Eden, October 1948; CSIRO B 3455 (4, 59–96 mm TL) off Moruya at "The Pines Close", 35°55' S, 150°10' E, 90 m, 28 April 1939. ***Victoria:*** AMS I.16987-006 (5, 75–150) Petersborough, estuary, near boat ramp, 38°37' S, 142°52' E, 6 m, 21 March 1972; CSIRO H 3793-03 (83) south of Gabo Island, 37°44.0' S, 149°58.0' E–37°42.3' S, 149°59.5' E, 108–115 m, 17 September 1994; NMV 30055 (502) Western Port, 38°22.2' S, 145°22.2' E, October 1858; NMV 43104 (375) Port Phillip Bay, Hobsons Bay, 37°52.2' S, 144°55.8' E, October 1878; NMV 43105 (375) Port Phillip Bay, Hobsons Bay, 37°52.2' S, 144°55.8' E, October 1879; NMV A842 (252) No location data, 1 January 1971; NMV A2941 (102) Port Phillip Heads, 38°16.8' S, 144°37.8' E, 1864; NMV A10567 (225) Western Port, 5 km north of Cowes, 38°26.1' S, 145°15.3' E, 20 m, 22 October 1986; NMV A23366-001 (438) no data, old collection. ***Tasmania:*** AMS I.17545-016 (70) Eaglehawk Neck, 43°2' S, 147°56' E, 29 November 1972; AMS I.17555-011 (6, 62–95) The Gardens, north of Binalong Bay, 41°13' S, 148°13' E, 1 m, 6 December 1972; AMS I.20086-001 (75) Spring Beach, 42°35' S, 147°54' E, 2–4 m, 16 December 1977; AMS I.34952-003 (260) Mouth of Fortescue Bay, 43°07'46" S, 147°59'28" E, 9–10 April 1994; CSIRO B 1259 (6, 50–62 mm TL) NE coast, 43°03' S, 148°03' E, 17 December 1976; CSIRO C 1405 (165) St Helens, 28 February 1951; CSIRO H 1151-02 (90) 40°55.05' S, 147°21.35' E, 33 m, 17 June 1987; CSIRO T 1105 (26) east of Babel Island, 120 m, 12 April 1984; CSIRO T 1252 (1) St Helens, 41°25' S, 148°16' E, 30 m; CSIRO T 1523 (1) St Helens Point, east coast of Tasmania, 25 February 1982; CSIRO T 1625-01 (27) Flinders Island; WAM P.27553.002 (103) Mercury Passage, 42°33' S, 147°57' E, 7–8 m; WAM P.27554.002 (2, 136–206) Spring Bay, 42°32' S, 147°55' E, 1–8 m; WAM P.27559.002 (2, 74–94) Saint Helens Point, 41°16' S, 148°22' E, 3 m; WAM P.27560.002 (2, 111–296) Bridport, 41°00' S, 147°23' E, 8–9 m; ***South Australia:*** AMS I.18470-005 (191) Robe, southwest coast, 37°10' S, 139°45' E, 1 m, 3 October 1975; AMS I.20180-021 (5, 69–112) Kangaroo Island, Penneshaw, 35°44' S, 137°58' E, 0–5 m, 9 March 1978; CSIRO CA 3516 (281 mm TL) west of Investigator Group, Great Australian Bight, 33°43.8' S, 132°07.8' E–33°45.1' S, 132°08.9' E, 180–184 m, 8 December 1981; SAMA AMSTAC102 (1) Great Australian Bight, Anxious Bay, 33°20'03" S, 134°38'47" E, 25 February 1981; SAMA AMSTAC181 (1) 30 miles west of Robe, 37°09'47" S, 139°12'31" E, 7 April 1981; SAMA AMSTAC213 (1) 4.5 miles west of Beachport, 37°29' S, 139°55' E, 8 April 1981; SAMA AMSTAC288 (1) Cape Buffon, 1 April 1981; SAMA AMSTAC289 (1) Cape Buffon, 1 April 1981; SAMA AMSTAC292 (1) 2 miles west of Cape Buffon, 1 April 1981; SAMA AMSTAC711 (1) Great Australian Bight, South East Isles, 34°20' S, 123°42' E, 26 July 1981; SAMA AMSTAC1331 (1) Spencer Gulf, between Wardang Island and Tipara Reef, 34°12'06" S, 137°18'24" E; SAMA AMSTAC1490 (1) Kangaroo Island, 2–3 miles off West Bay, 36°03'40" S, 137°12'39" E, 16 January 1982; SAMA AMSTAC1602 (1) off Port MacDonnell, 38°03'S, 140°42'E, 1 January 1982; SAMA F505 (1) 1918; SAMA F1012 (1) Gulf St Vincent, 35°10' S, 137°55' E, 1928; SAMA F1144 (1) 1928; SAMA 1145 (1); SAMA 1146 SAMA 1736 (1) St Vincent Gulf, Port Wakefield, 34°11' S, 138°29' E, 8 July 1932; SAMA F2011 (1) Spencer Gulf, Moonta, 34°3' S, 137°34' E, 14 October 1937; SAMA F2031 (1) Eyre Peninsula, Venus Bay, 33°12' S, 134°40' E, 29 April 1938; SAMA F2766 (1) Spencer Gulf, Port Lincoln, 34°44' S, 135°52' E, 28 January 1953; SAMA F3045 (1) Adelaide, Outer Harbour, 34°47' S, 138°29' E, 26 January 1962; SAMA F3377 (1) Kangaroo Island, Stokes Bay, 35°37' S, 137°12' E, 15 August 1966; SAMA F3392 (1) Kangaroo Island, Stokes Bay, 35°37' S, 137°12' E, 15 August 1966; SAMA F3649 (1) Kangaroo Island, Osmanli Reef, D'Estrees Bay, 35°59' S, 137°38' E, 13 August 1966; SAMA F3972 (1) near Coffin Bay, Farm Beach, 34°31' S, 135°23' E, 31 August 1974; SAMA F3980 (1) Encounter Bay, Port Elliott, Bashams Beach, 35°32' S, 138°41' E, 13 October 1974; SAMA F4093 (1) Encounter Bay, 35°33' S, 138°38' E,

20 July 1975; SAMA F4281 (1) Kangaroo Island, Emu Bay, 35°35' S, 137°31' E, 21 January1968; SAMA F5162 (1) Port MacDonnell, 38°3' S, 140°42' E, 1984; SAMA F5204 (1) Gulf St. Vincent, 34°26' S, 137°55' E, June 1984; SAMA F5529 (1) Kangaroo Island, Penneshaw, 35°43' S, 137°56' E, 29 October 1985; SAMA F6416 (1) Spencer Gulf, Cowell, 33°41' S, 136°55' E, 1988; SAMA F7174 (1) Spencer Gulf, 34°44' S, 135°52' E, 17 February 1993; SAMA F9097 (1) Kangaroo Island, north of Hog Bay, 35°43' S, 137°57' E, 20–22 m, 6 June 1954; SAMA F9576 (1) Investigator Strait, Althorpe Islands, 35°22'00" S, 136°52'00" E; SAMA F10526 (1) Investigator Strait, 17 km N of Point Marsden, 35°24'58" S, 137°38'15" E, 28 June 2001; SAMA F10723 (1) Great Australian Bight, 32°15'31" S, 132°39'15" E, 20 April 2002; SAMA F10749 (1) Great Australian Bight, 34°01'26" S, 134°28'34" E, 18 April 2002; SAMA F11194 (1) Gulf St Vincent, 35°16'54" S, 138°09'36" E, 17 May 2007; SAMA F11195 (1) Gulf St Vincent, 35°16'54" S, 138°09'36" E, 17 May 2007; SAMA F11196 (1) Gulf St Vincent, 35°16'54" S, 138°09'36" E, 17 May 2007; SAMA F14170 (1) Rivoli Bay, 37°31'44" S, 140°00'04" E, 6 April 2009. ***Western Australia:*** AMS I.12324 (225) Great Australian Bight, southwest of Eucla, 32°00' S, 128°00' E, September 1912; CSIRO H 4383-08 (72) Bunbury, inner harbour, general berth, 33°19.54' S, 115°39.57' E, 10.5 m, 6 March 1996; CSIRO H 4904-07 (108) Bunbury, outer harbour (disused jetty groyne), 3.5 m, 6 March 1996; NMV A9232 (350) Great Australian Bight, 120 km south of Middini Beach, 33°17.1' S, 127°29.7' E, 162–160 m, 14 February 1990; SAMA F73 (1) Abrolhos Islands, 28°45' S, 113°47' E, 22 April 1913; WAM P.1794.001 (365) Hopetoun, 33°57' S, 120°07' E; WAM P.7687.001 (350) Albany, 35°00' S, 117°52' E; WAM P.14596.001 (lost?) 31°54' S, 110°10' E; WAM P.26119.001 (149) Lookout Point, 34°53' S, 118°25' E; WAM P.29035.009 (270) 34°03' S, 122°00' E; WAM P.29339.001 (160) Mandurah. ***Tasman Sea:*** NMNZ P.009285 (280) southern Lord Howe Rise, 38° S, 168° E, 260 m, 7 December 1993; NMNZ P.030825 (460) southern Lord Howe Rise, 38° S, 168° E, 400–405 m, 31 August 1993; NMNZ P.031243 (540) southern Lord Howe Rise, 38° S, 168° E, 260 m, 7 December 1993. **New Zealand,** ***North Island:*** NMNZ P.000256 (135) Auckland, Hauraki Gulf, 36°30' S, 175°0' E, September 1920; NMNZ P.001236 (486) Wellington, Makara, 41°13.0' S, 174°42.5' E, 40 m, 28 February 1953; NMNZ P.001462 (528) Wellington, Cape Terawhiti, 41°17' S, 174°37' E, 9 m, 28 February 1954; NMNZ P.001970 (165) Bay of Plenty, northwest of Mayor Island, 37°15' S, 176°12' E, 146–219 m, 18 August 1956; NMNZ P.002233 (379) Wellington, North of Castle Point, 41°37' S, 175°16' E, 65 m, 25 September 1957; NMNZ P.002795 (500) Wellington, South of Titahi Bay, 41°6' S, 174°50' E, 3 m, 12 July 1959; NMNZ P.006783 (308) Wellington, Breaker Bay, Seatoun, 41°20' S, 174°50' E, 9 October 1973; NMNZ P.007789 (92) Hawke's Bay, 30 km east of Portland Island, 39°18.25' S, 178°12.00' E, 258–306 m, 27 January 1979; NMNZ P.008360 (116) Bay of Plenty, southeast of Mayor Island, 37°22.5' S, 176°22.0' E, 207–219 m, 27 February 1957; NMNZ P.008361 (8, 74–120) South Auckland, east-northeast of Tolaga Bay, 38°15.2' S, 178°38.6' E, 139 m, 16 January 1979; NMNZ P.009286 (2, 322–331) South Auckland, Anchor Reef, southeast corner Whale Island, 37°51' S, 176°59' E, 1 July 1998; NMNZ P.010327 (3, 315–352) Bay of Plenty, north of Mayor Island/east of Slipper Island, 37°4.95' S, 176°12.70' E, 315–352 m, 18 April 1981; NMNZ P.013608 (550) Wellington, Mana Island, 41°5' S, 174°52' E, 74 m, 12 March 1983; NMNZ P.014893 (2, 360–410) Three Kings Islands, NW Bay, Great Island, 34°9.0' S, 172°8.5' E, 14 m, 25 November 1983; NMNZ P.017924 (3, 42–48), off Mayor Island, Bay of Plenty, 37°14.35' S, 176°21.15' E, 218–225 m, 13 December 1975; NMNZ P.018168 (422) Bay of Plenty, off east side of Mayor Island, 37°18' S, 176°18' E, 37–91 m, 17 February 1986; NMNZ P.023405 (385) Gisborne, Waiaka Bay near Lottin Point, East Cape, 37°33' S, 178°9' E, 6 m, 24 June 1988; NMNZ P.028461 (288) Gisborne, southeast of Cape Runaway, East Cape, 37°32.9' S, 178°0.3' E, 8–12 m, 24 April 1992; NMNZ P.030132 (570) Gisborne, Monowai Reef, 38°35.9' S, 178°16.7' E, 15–21 m, 20 January 1993; NMNZ P.030137 (286) Gisborne, inside of Tuamotu Island, Gisborne Harbour, 38°42.2' S, 178°2.4' E, 4–7 m, 21 January 1993; NMNZ P.031312 (279) Hawke's Bay, 'White Cliffs', ~3 km south of Cape Kidnappers, 39°42' S, 177°3' E, 40 m, 23 January 1994; NMNZ P.031697 (200) Bay of Plenty, southern Kermadec Ridge, 37°32.90' S, 177°6.12' E, 325–327 m, 14 January 1995; NMNZ P.031923 (114) Bay of Plenty, southern Colville Ridge, 36°57.12' S, 176°15.90' E, 336–339 m, 9 January 1995; NMNZ P.033156 (340) Wellington, north end of Mana Island, 41°4.63' S, 174°47.40' E, 10–15 m, 8 March 1996; NMNZ P.033318 (160) Wellington, north end of Mana Island, 41°4.63' S, 174°47.40' E, 10–15 m, 8 March 1996; NMNZ P.033569 (245) Bay of Plenty, Long Point, Mahia Peninsula, 39°10' S, 177°49' E, 8 m, 4 January 1995; NMNZ P.034786 (520) Hawke's Bay, White Cliffs, northern end of Ocean Beach, 39°41' S, 177°3' E, 20 m, 27 April 1997; NMNZ P.036897 (440) South Auckland, Anchor Reef, southeast corner Whale Island, 37°51' S, 176°59' E, 1 July 1998; NMNZ P.036907 (375) South Auckland, east side of White Island, 37°31' S, 177°12' E, 160 m, 4 July 1998; NMNZ P.041342 (380) Northland, 232 m, 25 January 2005. ***South Island:*** NMNZ P.005345 (2, 127) Nelson, Central Eastern Challenger Plateau, west of Farewell Spit, 40°37.5' S, 171°37.5' E, 247 m, 3 March 1971; NMNZ P.007707 (353) Canterbury, Mernoo Bank, 43°23.0' S, 175°6.8' E, 124–129 m, 12 January 1979; NMNZ P.008031 (489) Marlborough, Kaikoura region, 42°25' S, 173°43' E, 109–128 m; NMNZ P.009008 (2, 290–380) Westland, Hokitika Canyon, 42°13' S, 170°34' E, 305–380 m, 12 August 1979; NMNZ P.009465 (420) Marlborough, Kaikoura region, 42°25' S, 173°43' E; NMNZ P.016345 (300) Snares Islands, off North Promontory, 48°0' S, 166°36' E, 110 m, 5 December 1984; NMNZ P.016889 (422) Southland, west of Richards Point, Bradshaw Sound, Fiordland, 45°16.7' S, 167°0.7' E, 15–21 m, 27 February 1985; NMNZ P.016933 (2, 150–177) Southland, off Seymour Island, Doubtful Sound, Fiordland, 45°18' S, 167°0' E, 12 m, 28 February 1985; NMNZ P.016970 (460) Southland, off Seymour Island, Doubtful Sound, Fiordland, 45°18' S, 167°0' E, 12 m, 28 February 1985; NMNZ P.017874 (65) Westland, NW off Hokitika, 40°38.48' S, 170°11.42' E, 169 m, 11 December 1978; NMNZ P.021159 (620) Southland, mouth of Caswell Sound, Fiordland, 44°58.9'

S, 167°7.6' E, 48 m, 15 February 1987; NMNZ P.023949 (430) Stewart Island, off Hebe Island, Port Pegasus, 47°11.8' S, 167°38.5' E, 10–16 m, 28 January 1989; NMNZ P.027612 (2, 195–256) Stewart Island, SE Point Rosa Island, Port Pegasus, 47°9.9' S, 167°42.0' E, 0–9 m, 10 March 1992; NMNZ P.027622 (390) Stewart Island, 13 Fathom Point, Whale Passage, Port Pegasus, 47°11.00' S, 167°43.05' E, 20 m, 13 March 1992; NMNZ P.027870 (225) Stewart Island, SE Point Rosa Island, Port Pegasus, 47°9.9' S, 167°42.0' E, 0–9 m, March 1992; NMNZ P.030270 (133) Southland, 'Little Cove', Acheron Passage, Fiordland, 45°39.88' S, 166°44.78' E, 0–10 m, 21 March 1993; NMNZ P.030520 (320) Southland, "46 fathom point", Broughton Arm, Breaksea Sound, Fiordland, 45°33.35' S, 166°57.95' E, 2–18 m, 21 March 1993; NMNZ P.030554 (330) Southland, Peninsula opposite Oak Island, Wet Jacket Arm, Fiordland, 45°38.65' S, 166°51.90' E, 0–33 m, 28 March 1993; NMNZ P.030559 (310) Southland, Stephens Cove, Fiordland, 45°36' S, 166°40' E, 7 m, 18 March 1993; NMNZ P.030940 (3, 84–183) Tasman, Taupo Point, Abel Tasman National Park, 40°47.5' S, 172°57.0' E, 4–8 m, 19 November 1993; NMNZ P.032260 (157) Southland, 1 nautical mile south of Deas Cove, south side of Thompson Sound, Fiordland, 45°12.79' S, 166°57.31' E, 8–24 m, 28 March 1995; NMNZ P.033439 (475) Stewart Island, south of Stewart Island, Campbell Plateau, 48°47.78' S, 166°47.26' E, 158 m, 5 March 1996; NMNZ P.035083 (140) Westland, Bridget Point, Milford Sound; Fiordland, 44°38.61' S, 167°54.86' E, 6–14 m, 5 April 1998; NMNZ P.035981 (462) Westland, point south of Teer Creek, 44°0' S, 168°29' E, 15–18 m, 13 February 1999. ***Chatham Rise:*** NMNZ P.020957 (2, 265) east of Chatham Islands, 43°30.95' S, 176°9.25'W, 176–205 m, 22 May 1987; NMNZ P.021008 (378) east of Chatham Islands, 43°31' S, 176°7'W, 206–226 m, 24 May 1987; NMNZ P.026557 (5, 143–255) channel between Point Munning and Te Whakuru Island, Chatham Island, 43°44.3' S, 176°12.0'W, 0–3 m, 15 February 1991; NMNZ P.026670 (245) Cape Fournier, Owenga, Chatham Island, 44°2.0' S, 176°19.5'W, 15–17 m, 10 February 1991; NSMT 32967 (537) Wanganella Bank, 32°41.6' S, 167°42' E, 123–405m, 12 December 1989.

Pseudophycis breviuscula

(636 specimens, 15–196 mm SL). **Australia,** ***New South Wales:*** AMS I.3982 (152) off Newcastle, 32°56' S, 151°56' E, 4 March 1898; AMS I.3983 (170) off Newcastle, 32°58' S, 151°55' E, 4 March 1898; AMS A.10105 (138) Port Jackson, 33°50' S, 151°10' E, 1881; AMS I.16879-001 (105) Jervis Bay, off Darling Road, 35°3' S, 150°44' E, 22 September 1971; AMS I.17178-016 (65) Port Jackson, near Manly, 33°50' S, 151°16' E, 13 August 1972; AMS I.19893-024 (4, 67–128) south of Nadgee River mouth, north end of Blackpoint, 37°30' S, 149°58' E, 0–5 m, 26 August 1976; AMS I.20065-002 (27, 35–46) off Ulladulla, 35°21' S, 150°49' E, 0–250 m, 27 October 1977; AMS I.20472-002 (2, 40-43) east of Green Cape, 36°24' S, 150°18' E, 0–128 m, 1 November 1977; AMS I.20568-002 (2, 130–170) east of Tweed Heads, 28°14' S, 153°50' E, 132–137 m, 2 June 1978; AMS I.20653-008 (119) and AMS I.20653-013 (59) east of Hat Head, 31°5' S, 31°2' S, 153°13' E, 155 m, 24 August 1977; AMS I.21366-019 (5, 35–45) off Newcastle, 33°17' S, 153°5' E, 28 November 1979l; AMS I.21797-003 (127) east of Tuggerah Lake, 33°8' S, 151°54' E, 115 m, 17 July 1978; AMS I.21798-002 (4, 100-120) east of Tweed Heads, 28°14' S, 153°50' E, 132–137 m, 2 June 1978; AMS I.22873-002 (115) southeast of Cape Byron, 28°43' S, 153°49' E, 131 m, 1 November 1978; AMS I.23379-006 (42) Coffs Harbour, boat harbour, 30°20' S, 153°20' E, 0–6 m, 3 May 1977; AMS I.23685-001 (132) Smoky Cape, Coffs Harbour, Scott Point, Nambucca Heads, 30°43' S, 153°16' E, 134–151 m, 10 October 1978; AMS I.23687-001 (82) Ballina - Tweed Heads, 28°4' S, 153°50' E, 137 m, 16 August 1978; AMS I.23688-001 (3, 117–165) Ballina - Tweed Heads, east of Brunswick Heads, 28°25' S, 153°48' E, 119 m, 3 June 1978; AMS I.23692-001 (2, 122–145) Ballina - Tweed Heads, 28°34' S, 153°50' E, 146–150 m, 18 August 1978; AMS I.23870-006 (106) Sydney-Newcastle, 33°40' S, 152°56' E, 720 m, 20 December 1976; AMS I.24367-003 (2, 37–48) off Sydney, 33°43' S, 151°54' E, 430–541 m, 27 October 1983; AMS I.24440-002 (4, 35-45) east of Twofold Bay, 37°03' S, 150 20' E, 149 m, 1 November 1977; AMS I.25865-003 (145) off Port Stephens, 32°49' S, 152°2' E, 40–46 m, 10 April 1985; AMS I.25893-001 (196) off Twofold Bay, 37°5' S, 149°55' E, 18–46, 25 November 1984; AMS I.26239-005 (118) east of Wooli, 29°49' S, 153°24' E, 36–54 m, 25 March 1985; AMS I.26444-002 (112) northeast of Broken Bay, 33°29' S, 151°49' E, 142–137 m, 13 March 1986; AMS I.26451-005 (4, 51–99) Sydney, off Broken Bay, 33°35' S, 151°41' E, 134–135 m, 10 February 1986; AMS I.26906-009 (93) Iluka, 29°24' S, 153°21' E, 1987; AMS I.26919-002 (42) northeast of Jervis Bay, off Point Perpendicular, 35°5' S, 150°55' E, 128 m, 13 December 1984; AMS I.27064-006 (91) 35°0' S, 150°45' E, 2–7 m, January 1987; AMS I.27179-010 (43) 30°40' S, 159°0 E, 0–229 m, 20 September 1987; AMS I.27322-005 (141) off Tuncurry, 32°08' S, 152°31' E, 1 October 1985; AMS I.27323-004 (104) east of Camden Head, 31°42' S, 152°49' E, 2 October 1985; AMS I.27670-001 (93) off Coffs Harbour, 30°26' S, 153°22' E, 25 July 1981; AMS I.31483-003 (135) off Evans Head, 29°00' S, 153°49' E, 6 May 1990; AMS I.32120-001 (109) off Clarence River, 29°24' S, 153°35' E, 1–2 May 1990; AMS I.34467-001 (2, 143–162) off Wollongong, 34°28' S, 151°2' E, 100 m, 6–7 May 1993; AMS I.34472-002 (3, 90–150) off Wollongong, 34°26' S, 150°58' E, 7–8 May 1993; AMS I.34474-001 (94) off Wollongong, 34°28' S, 151°2' E, 100 m, 7–8 May 1993; AMS I.34475-001 (128) off Wollongong, 34°28' S, 151°2' E, 100 m, 7–8 May 1993; AMS I.34557-003 (96) off Wollongong, 34°26' S, 150°57' E, 50 m, 6–7 May 1993; AMS I.34715-001 (2, 85–115) Botany Bay channel off revetment, 33°59' S, 151°12' E, 16 December 1978; AMS I.34894-001 (125) off Wollongong, 34°0' S, 151°0' E, 28–29 March 1994; AMS I.35422-001 (2, 95–120) northeast of Coffs Harbour, 30°15.75' S, 153°21.98' E, 98 m, 12–13 August 1993; AMS I.35424-001 (3, 120–135) east of Coffs Harbour, 30°17' S, 153°13' E, 50 m, 8–9 September 1994; AMS I.35427-001 (2, 86–93) east of Coffs Harbour, 30°17' S, 153°13' E, 50 m, 9 September 1994; AMS I.40321-006 (130) southeast of Yamba, 29°39' S, 153°41' E, 5 July 1999; AMS I.40491-001 (6, 84–125) off Wollongong, 32°26' S, 150°57' E, 50 m, 6–7 May 1993;

AMS I.44627-019 (79) Tathra, Baronda Headland, south side, 36°41'11" S, 149°59'54" E, 8 April 2008; AMS I.44627-020 (81) Tathra, Baronda Headland, south side, 36°41'11" S, 149°59'54" E, 8 April 2008; AMS I.44632-006 (2, 100) Tathra, Kianniny boat ramp, 36°44'15" S, 149°58'60" E, 9 April 2008; AMS I.44823-022 (97) north side of Moon Island, 33°05'12" S, 151°40'16" E, 5 May 2009; AMS I.45025-004 (4, 96–115) Colliers Beach, inlet near Mollymook Golf Course, 35°20'46" S, 150°28'36" E, 10 March 2010; AMS I.45025-005 (2, 100–115) Colliers Beach, inlet near Mollymook Golf Course, 35°20'46" S, 150°28'36" E, 10 March 2010; AMS I.45027-018 (2, 65–75) Jones Beach, Mollymook, 35°19'19" S, 150°29' E, 11 March 2010; AMS I.45633-057 (6, 71–95) Washerwomans Beach, 35°14'39" S, 150°32'09" E, 16 March 2011; AMS IA.1955 (72) off Green Cape, 13–35 km northeast of cape, 37°4' S, 150°9' E, 71–84 m, June 1924; AMS IA.1956 (80) and AMS IA.1957 (60) 13–35 km northeast of Green Cape, 37°4' S, 150°9' E, 71–84 m, June 1924; AMS IA.2966 (125) 16–19 km northeast of Sydney Harbour, 33°' S, 151°E, 110–146 m, 1926; AMS IA.6898 (75) 5 km off Broughton Island, 32°37' S, 152°22' E, 82–91 m, 29 May 1936; AMS IB.4359 (110) east of Tuggerah Lakes, 33°20' S, 151°35' E, 229–260 m, 19 June 1959; AMS IB.7005 (147) off Port Stephens, 32° S, 152° E, 1964; CSIRO A 1622 (84 mm TL) Pambula Bay, 11 m, 13 May 1950; CSIRO A 1639 (97 mm TL) Twofold Bay, off Eden, 10.8 m, 5 May 1950; CSIRO A 1640 (83 mm TL) Twofold Bay, off Eden, 10.8 m, 5 May 1950; CSIRO H 3575-01 (2, 60–70) east of Merimbula, 36°55.4' S, 149°56.8' E–36°54.6' S, 149°58.0' E, 33–40 m, 4 August 1993; CSIRO H 4258-04 (107) south of Green Cape, 37°21.23' S, 150°06.03' E–37°20.1' S, 150°06.52' E, 90–94 m, 7 May 1996; CSIRO H 4773-01 (148) east of Yamba, 29°24' S, 153°35' E–29°23' S, 153°35' E, 68–71 m, 17 April 1996; CSIRO H 4773-02 (4, 132–158) east of Yamba, 29°24' S, 153°35' E–29°23' S, 153°35' E, 68–71 m, 17 April 1996; CSIRO H 5962-01 (2, 105–142) northeast of Coffs Harbour, 29°50' S, 153°27' E–29°48' S, 153°27' E, 66–68 m, 15 April 1996; CSIRO H 6838-08 (4, 103–160) east of Broken Bay, 33°32.3' S, 151°30.9' E–33°28.3' S, 151°32.5' E, 60–62 m, 27 June 2006; CSIRO H 6845-01 (3, 117–181) east of Broken Bay, 33°29.4' S, 151°32.2' E–33°33.7' S, 151°29.8' E, 60–62 m, 29 June 2006; CSIRO T 1434 (1) off Port Stephens, 32°44' S, 152°16' E–32°43' S, 152°23' E, 83–104 m, 20 August 1979; NMV A6437 (31.0) 65 km east of Nowra, 34°52.9' S, 151°22.7' E, 23 October 1988; NMV A6438 (31.3) 52 km east-southeast of Nowra, 34°56.1' S, 151°14.7' E, 21 October 1988; NMV A13051 (2, 52.4–68.5) 12 km east-northeast of Bermagui, 36°23.3' S, 150°10.7' E, 72–69 m, 15 August 1993. ***Victoria:*** NMV A7531 (55.9) Batison Point, tide pool, 37°34.2' S, 149°46.2' E, 1 m, 6 April 1989; NMV A7560 (55.9) Gabo Island, harbour on southeast side, 37°34.2' S, 149°55.2' E, 4 m, 4 April 1989; NMV A13050 (68.8) Disaster Bay, 37°16.3' S, 149°57.9' E, 24–29 m, 11 August 1993; NMV A2682 (28.1) central Bass Strait, 26 km southeast of Aireys Inlet, 38°39.8' S, 144°18.2' E, 79 m, 19 November 1981; NMV A3776 (2, 72.2–77.2) eastern Bass Strait, 24 km southwest of Lakes Entrance, 38°03' S, 147°49.8' E, 45 m, 1 October 1983; NMV A3841 (4, 58.9-79.3) eastern Bass Strait, 28 km south-southwest of Marlo, 37°58.8' S, 148°27' E, 51 m, 30 July 1983; NMV A5812 (3, 46.8–61.8) eastern Bass Strait, 40 km south-southwest of Lakes Entrance, 38°18' S, 147°37' E, 55 m, 31 July 1983; NMV A835 (108) Bass Strait, 24 km (16 miles) south-southwest of Lakes Entrance, 38°7' S, 147°51.8' E, 29–37 m, 27 April 1948; NMV A8775 (38.3) Bass Strait, 30 km east of Gabo Island, 37°37.2' S, 150°16.7' E, 432 m, 14 October 1984; NMV A20817 (74.5) southeast of Lakes Entrance, 38°10.2' S, 148°4.8' E, 1971; NMV A20818 (4, 48.3–80.0) no collection data; NMV A29091-001 (80.5) Portland, inner harbour, South Henty, 38°21' S, 141°36' E, 13 m, 1 May 1996. ***Tasmania:*** AMS I.43935-001 (78) East of Fortescue Bay, north of Hippolyte Rocks, 43°06'42" S, 148°03'27" E, 9–10 April 1994; CSIRO H 6980-04 (42) southern Tasman Sea, 40°48.97' S, 150°58.30' E–40°49.16' S, 150°56.54' E, 392–185 m, 21 June 2009; CSIRO H 6991-01 (36) southern Tasman Sea, 40°48.35' S, 152°16.42' E–40°48.53' S, 152°15.25' E, 174–91 m, 21 June 2009; CSIRO T 1952 (150) Frederick Henry Bay, 25 m, 19 September 1983; NMV A2626 (47.2) eastern Bass Strait, 100 km northeast of North Point, Flinders Island, 38°52.6' S, 148°25.2' E, 130 m, 15 November 1981; NMV A2676 (35.4) central Bass Strait, 35 km north of Cape Wickham, King Island, 39°13.6' S, 143°55.6' E, 85 m, 23 November 1981; NMV A3789 (40.7) eastern Bass Strait, 18 km north-northeast of Deal Island, 39°19.2' S, 147°27' E, 63 m, 1 October 1983; NMV A6435 (25.8) 68 km east of Cape Tourville, 42°3.9' S, 149°11.9' E, 27 October 1988; NMV A6439 (2, 24.3–34.0) 52 km east-northeast of Cape Tourville, 42°2.4' S, 148°58.3' E, 28 October 1988; NMV A6440 (3, 17.7–22.2) 54 km east-northeast of Cape Tourville, 42°02.1' S, 148°58.4' E, 28 October 1988; NMV A6909 (30.5) 78 km south of Point Hicks, 38°30.1' S, 149°15.5' E, 25 October 1988; NMVA26688-003 (2, 65.0–76.4) Port Phillip Bay, off Seaford, artificial reef, 38°05.25' S, 145°05.95' E; NMV A31158-001 (101) Port Phillip Bay, off Carrum, 7 April 2011; NMV A31159-001 (95.5) and NMV A31159-002 (87.9) Port Phillip Bay, 28 March 2011; WAM P.27554.021 (127) Spring Bay, 42°32' S, 147°55' E, 1–8 m. ***South Australia:*** AMS I.20167-021 (69) Kangaroo Island, Knob Point, 2 km east of Stokes Bay, 35°37' S, 137°15' E, 15 m, 5 March 1978; AMS I.20168-013 (77) Kangaroo Island, Hanson Bay, 36°01' S, 137°52' E, 6 March 1978; AMS I.20171-022 (41) Kangaroo Island, Vivonne Bay, 36°0' S, 137°11' E, 0–2 m, 6 March 1978; CSIRO H 5337-01 (2, 73–86) Great Australian Bight, 33°16.00' S, 130°43.15' E–33°16.60' S, 130°48.63' E, 137 m, 11 May 2000; CSIRO H 5338-01 (4, 69–125) Great Australian Bight, 31°50.05' S, 130°45.90' E–31°50.32' S, 130°45.10' E, 55 m, 14 May 2000; SAMA AMSTAC589 (4) Great Australian Bight, 8 nautical miles south of Point Weyland, 33°22'49" S, 134°37'53" E, 18 September 1981; SAMA AMSTAC1660 (1) Great Australian Bight, 6 miles off Venus Bay, 33°18'S, 134°35'E, 1 July 1982; SAMA F3948 (1) northern Great Australian Bight, 32°24' S, 133°30' E, 42 m, 5 May 1973; SAMA F9096 (1) Kangaroo Island, Nepean Bay, 35°38' S, 137°46' E, 54 m, 28 April 1981; SAMA F9098 (1) Great Australian Bight, Anxious Bay, 33°20'03" S, 134°38'47" E, 25 February 1981; SAMA F9099 (1) Great Australian Bight, Nuyts Archipelago, off Goat Island, 32°17'00" S, 133°30'00" E, 40 m, 28 February 1981;

SAMA F10955 (1) Investigator Strait, 35°26'43" S, 137°56 42" E, 17 May 2007; SAMA F10990 (1) Investigator Strait, 35°24'28" S, 137°54'40" E, 17 May 2007; SAMA F14583 (1) 22 May 1905. ***Western Australia:*** AMS I.20229-021 (90) Cockburn Sound, 1 km south of Carnac Island, 32°10' S, 115°40' E, 6–8 m, 26 March 1978; AMS I.20247-010 (2, 58–63) Rottnest Is, Kingston Reefs, 31°59' S, 115°33' E, 12 April 1978; CSIRO H 4384-01 (110) Albany, Princess Royal Harbour, 35°02.02' S, 117°53.05' E, 7 m, 28 February 1996; WAM P.2999.001 (120) Mandurah, 32°32' S, 115°43' E; WAM P.7409.001 (174) Augusta, 34°19' S, 115°09' E; WAM P.21913.001 (135) Wilson Inlet, 34°59' S, 117°26' E; WAM P.25195.019 (3, 47–56) Cape Naturaliste, 33°32' S, 115°02' E, 1–5 m; WAM P.26006.003 (46) 34°07' S, 122°16' E, 13 m; WAM P.26009.006 (2, 65–70) Lucky Bay, 34°00' S, 122°14' E, 13 m; WAM P.26600.008 (4, 30–76) Albany, 35°08' S, 117°38' E; WAM P.26608.016 (2, 50–75) Cheyne Beach, 34°53' S, 118°25' E, 12–15 m; WAM P.26621.003 (117) Porpoise Bay, 32°00' S, 115°30' E, 1 m; WAM P.28292.008 (9, 45–121) Lucky Bay, 34°00' S, 122°14' E, 7–10 m; WAM P.28293.011 (67) Lucky Bay, 34°00' S, 122°14' E, 5–7 m; WAM P.28296.013 (5, 45–96) 34°08' S, 122°15' E, 5–6 m; WAM P.28298.004 (24, 42–118) Lucky Bay, 34°08' S, 122°15' E, 24 m; WAM P.28513.006 (92) Duke of Orleans Bay, 33°54' S, 122°37' E, 8 m; WAM P.28523.006 (3, 38–70) Augusta, 34°19' S, 115°10' E, 12–13 m. **New Zealand,** ***North Island:*** AMS I.18281-005 (6, 75–90) Auckland, Goat Island, 18 m, 1975; AMS I.18282-003 (8, 65–105) Auckland, Goat Island, 57°S, 168°E, 20 m, 31 March 1975; NMNZ P.002281 (4, 80–106) southeast of Mayor Island, 37°22.50' S, 176°22.00' E, 207–219 m, 27 February 1957; NMNZ P.002289 (69) south of Mayor Island, 37°19.5' S, 176°16.5' E, 102 m, 27 February 1957; NMNZ P.002299 (102) Manakau Harbour, above Weymouth, 37°2.45' S, 174°50.25' E, 0–5 m, 5 January 1957; NMNZ P.003151 (10, 78–117) Urupukapuka Island, Bay of Islands, 35°12.32' S, 174°14.40' E, 2–7 m, February 1961; NMNZ P.003616 (2, 73–79) 22.5 km east of White Island, 37°30' S, 177°26' E, 192 m, 3 April 1963; NMNZ P.003756 (130) Napier breakwater, 39°28.50' S, 176°55.25' E, 9 m, March 1964; NMNZ P.005275 (132) off Kaipara Harbour, 36°26.0' S, 173°50.5' E, 115 m, 9 January 1971; NMNZ P.005866 (2, 93–109) northeast of Motiti Island, 37°39' S, 176°33' E, 64 m, 14 April 1972; NMNZ P.005969 (2, 93–99) main channel off Kopumiti Point, Whangaroa Harbour, 35°2' S, 173°45' E, 9–15 m, 22 February 1974; NMNZ P.006801 (75) northern Taranaki Bight, Aotea Seamount, 38°13.5' S, 173°54.0' E, 135–137 m, 13 November 1971; NMNZ P.007794 (8, 51–72) 9 km north of Motuhara Island, 37°48.15' S, 177°1.10' E, 72–84 m, 20 January 1979; NMNZ P.007865 (10, 60–83) north of Mayor Island, 37°10.90' S, 176°10.75' E, 198–273 m, 22 January 1979; NMNZ P.007899 (3, 55–110) between Motuhara Island and Rurima Inlets, 37°51.75' S, 176°55.90' E, 34–39 m, 21 January 1979; NMNZ P.008349 (4, 68–121) north of Mayor Island, 37°10.90' S, 176°10.75' E, 198–273 m, 22 January 1979; NMNZ P.008362 (9, 54–79) east-northeast of Tolaga Bay, 38°15.2' S, 178°38.6' E, 139 m, 16 January 1979; NMNZ P.008364 (12, 15–86) off Mayor Island, 37°9.1' S, 176°24.4' E, 753–826 m; NMNZ P.008461 (108) off Kohinga point, Bay of Islands, 35°10' S, 174°10' E, 8 December 1973; NMNZ P.008463 (74) Goat Island, Leigh, 36°16' S, 174°48' E, 1970; NMNZ P.008472 (120) Whatawhiwhi, Doubtless Bay, 34°53.00' S, 173°24.25' E, 17 November 1963; NMNZ P.009003 (2, 73–76) Spirits Bay, Northland, 34°27' S, 172°50' E, 4 m, 14 November 1963; NMNZ P.009796 (56) southeast of Three Kings Islands, 34°20.2' S, 172°21.8' E, 121 m, 2 February 1981; NMNZ P.009802 (75) Ranfurly Bank, East Cape, 37°38.4' S, 178°51.7' E, 79–83 m, 22 January 1981; NMNZ P.009809 (3, 49–71) off Ninety Mile Beach, 34°41.9' S, 172°33.5' E, 103 m, 10 January 1981; NMNZ P.009813 (61) off Raglan Harbour, 37°48.0' S, 174°14.7' E, 103 m, 13 January 1981; NMNZ P.009817 (4, 68–90) off Parengarenga Harbour, 34°32' S, 173°6' E, 93–102 m, 27 January 1981; NMNZ P.009828 (6, 59–122) northwest Ahipara, 34°50.0' S, 172°46.1' E, 90 m, 10 January 1981; NMNZ P.010431 (63) off Mahia Peninsula, 39°10' S, 178°0' E, 15 m, 14 April 1981; NMNZ P.011874 (95) 2.4 km west of Cape Colville, Hauraki Gulf, 36°37' S, 175°28' E, 40–70 m, 17 February 1976; NMNZ P.012089 (58) northeast of Ninepin Rock, Bay of Islands, 35°8.8' S, 174°10.9' E, 66–79 m, 1 December 1971; NMNZ P.012091 (103) North Cape, 34°25' S, 173°3' E, 109–146 m, 8 October 1964; NMNZ P.012093 (108) north of the Noises, Hauraki Gulf, 36°42' S, 174°58' E, 46 m, 17 May 1965; NMNZ P.014301 (12, 72–120) Matai Bay, south side of middle headland, Othngahunga Bay, 34°50' S, 173°25' E, 7–13 m, 18 August 1983; NMNZ P.014349 (2, 90–97) Waikato Bay, south end of Matai Bay, Northland, 34°50' S, 173°25' E, 3–5 m, 19 August 1983; NMNZ P.014380 (2, 100–109) north end of Taupo Bay, 34°59.17' S, 173°43.00' E, 7–8 m, 20 August 1983; NMNZ P.014397 (3, 75–92) Oakura Bay, Northland, 35°23' S, 174°21' E, 4–6 m, 21 August 1983; NMNZ P.015199 (108) channel between Henry Island and Cape Home, Oakura Bay, 35°23.0' S, 174°22.2' E, 14–17 m, 23 February 1984; NMNZ P.015305 (110) south of Tutukaka Harbour entrance, Northland, 35°37.36' S, 174°32.55' E, 13 m, 19 February 1984; NMNZ P.016983 (34) seawater intake, New Plymouth Powerhouse, 39°3' S, 174°5' E, 1983; NMNZ P.018115 (110) off marine laboratory, Island Bay, 41°21' S, 174°45.89' E, 15 m, 22 January 1986; NMNZ P.018200 (3, 80–111) reef in northern Crater Bay; Mayor Island, 37°17.2' S, 176°16.4' E, 12 m, 19 February 1986; NMNZ P.018223 (96) Mount Manganui, Bay of Plenty, 37°37.5' S, 176°10.4' E, 0–3 m, 13 February 1986; NMNZ P.018258 (88) Tauranga Bay, Mayor Island, 37°18.4' S, 176°15.8' E, 12 m, 18 February 1986; NMNZ P.018290 (3, 62–100) off Rabbit [Motuotou] Island, Mount Maunganui, 37°38.0' S, 176°11.6' E, 6–15 m, 14 February 1986; NMNZ P.021081 (7, 83–134) off Bell Block, New Plymouth, 39°1' S, 174°9' E, 9 m, 13 December 1986; NMNZ P.021541 (4, 52–83.2) rocks off Whangamata Beach, Coromandel, 37°12.88' S, 175°53.65' E, 17 m, 29 November 1987; NMNZ P.021645 (72.8) east side of Great Mercury Island, Coromandel, 36°37.05' S, 175°50.23' E, 15 m, 2 December 1987; NMNZ P.021767 (3, 59–89.3) pools between Jackson and Fantail Bays, Coromandel, 36°32' S, 175°20' E, 0–3 m, 8 December 1987; NMNZ P.021797 (10, 72.1–99.8) rocks off Whangamata Beach, Coromandel, 37°12.88' S, 175°53.65' E, 17 m, 29 November 1987; NMNZ P.021883 (95)

Firth of Thames, 37°0' S, 175°20' E, 30 January 1965; NMNZ P.023179 (93) Matakaoa, East Cape, 37°34' S, 178°20' E, 16 m, 25 June 1988; NMNZ P.023211 (6, 81–113) Waiaka Bay near Lottin Point, East Cape, 37°33' S, 178°9' E, 6 m, 24 June 1988; NMNZ P.024349 (72) Higgins Wharf, Napier, 39°30' S, 176°50' E, 22 March 1988; NMNZ P.026295 (110) Charity Reef, Pourerere, 40°6.2' S, 176°53.5' E, 12 m, 19 January 1991; NMNZ P.026356 (66) Pauanui Point Reef, East Coast, 40°4.4' S, 176°53.8' E, 7–10 m, 16 January 1991; NMNZ P.028100 (4, 59–120) Okakari Point, Northland, 36°15' S, 174°46' E, 2–3 m, 9 April 1992; NMNZ P.028204 (5, 86–151) Midway Point, south of Lottin Point, East Cape, 37°32.6' S, 178°12.9' E, 15–17 m, 2 May 1992; NMNZ P.028237 (5, 59–110) west side of Orete Point, Te Kaha, 37°35.25' S, 177°53.15' E, 11–12 m, 3 May 1992; NMNZ P.028271 (2, 95–131) bay west of Lottin Point, Waiaka Bay, East Cape, 37°32.9' S, 178°8.7' E, 15–20 m, 1 May 1992; NMNZ P.028389 (2, 62–68) south of Tohora Pirau, Lottin Point, 37°32.7' S, 178°10.0' E, 7–10 m, 2 May 1992; NMNZ P.028428 (4, 74–87) Kaipiro Reef, Maraetai Bay, Te Kaha, Bay of Plenty, 37°42.6' S, 177°41.7' E, 19–21 m, 30 April 1992; NMNZ P.028460 (98) Kaipiro Reef, Maraetai Bay, Te Kaha, Bay of Plenty, 37°42.6' S, 177°41.7' E, 19–21 m, 30 April 1992; NMNZ P.029790 (2, 105–130) off Horoera Point, East Cape, 37°37.8' S, 178°28.9' E, 8–10 m, 24 January 1993; NMNZ P.029846 (2, 57–64) between Moutahiauru Island and Koutunui Head, East Cape, 38°3.35' S, 178°22.20' E, 9 m, 25 January 1993; NMNZ P.029855 (3, 60–75) Whanarua Bay, Bay of Plenty, 37°40.0' S, 177°46.7' E, 15–21 m, 28 January 1993; NMNZ P.029875 (2, 62–75) between Te Araroa and Horoera, East Cape, 37°37.6' S, 178°25.0' E, 0–3 m, 24 January 1993; NMNZ P.029969 (8, 45–65) northeast Waipiro Bay, East Cape, 38°0.0' S, 178°23.1' E, 21 m, 25 January 1993; NMNZ P.030070 (3, 63–120) Tatapouri Beach, Gisbourne, 38°39.2' S, 178°9.9' E, 6–8 m, 22 January 1993; NMNZ P.030121 (5, 60–75) eastern Whanarua Bay, Bay of Plenty, 37°40.5' S, 177°47.4' E, 8 m, 28 January 1993; NMNZ P.030607 (2, 70–117) Port of Napier, 39°28' S, 176°55' E, 23 March 1993; NMNZ P.030609 (7, 70–92) Gisborne Wharf, Poverty Bay, 38°40.5' S, 178°1.5' E, 8 m, 4 December 1992; NMNZ P.030615 (3, 78–117) Gisborne Wharf, Poverty Bay, 38°41' S, 178°2' E, 18 May 1993, NMNZ P.030617 (2, 62–73) Gisborne Wharf, Poverty Bay, 38°40' S, 178°1' E, March 1993; NMNZ P.030631 (4, 71–104) Port of Napier, 39°29' S, 176°55' E, 25 June 1993; NMNZ P.030685 (2, 87–106) Port of Napier, 39°21.9' S, 176°54.1' E, 5 m, 22 September 1992; NMNZ P.030692 (19, 49–103) Gisborne Wharf, Poverty Bay, 38°40.8' S, 178°1.1' E, 23 June 1993; NMNZ P.033570 (119) Long Point, Mahia Peninsula, 39°10' S, 177°49' E, 8 m, 4 January 1995; NMNZ P.033644 (6, 50–110) Whangawehi, Mahia Peninsula, 39°7' S, 177°54' E, 14 m, 25 January 1995; NMNZ P.034527 (90) off Great Exhibition Bay, Northland, 34°40.4' S, 173°31.0' E, 182 m, November 1977; NMNZ P.035537 (10, 77–105) Archway, east end of Whale (Moutohora) Island, 37°51.44' S, 176°59.39' E, 12–17 m, 1 June 1998; NMNZ P.035560 (3, 90–140) Rurima Islets, 37°49.78' S, 176°52.63' E, 7–10 m, 2 June 1998; NMNZ P.035584 (8, 82–139) North Bay, Whale (Motuhora) Island, 37°51.05' S, 176°58.57' E, 13–15 m, 3 June 1998; NMNZ P.036587 (23, 66–112) south Whale (Motuhora) Island, 37°51.70' S, 176°58.43' E, 8–12 m, 22 April 1999; NMNZ P.036641 (8, 82–118) Nursery Cove, White Island, 37°31.42' S, 177°10.37' E, 5–16 m, 23 April 1999; NMNZ P.036667 (7, 77–94) off Homestead Point, White Island, 37°31.77' S, 177°10.68' E, 8–14 m, 23 April 1999; NMNZ P.036698 (5, 77–116) west end of White Island, 37°51.05' S, 176°57.63' E, 12–16 m, 24 April 1999; NMNZ P.036723 (22, 65–95) southeast MacEvans Bay; Whale (Motuhora) Island, 37°51.57' S, 176°59.12' E, 12–17 m, 26 April 1999; NMNZ P.048348 (2, 62.1–67.9) off Kaweura, midway between South Head, Omapere and Maunganui Bluff, 35°38.14' S, 173°26.09' E, 0–10 m, 14 February 2011; NMNZ P.048431 (65.8) first coast beach south of southern headland of Hokianga Harbour, 35°32.93' S, 173°22.01' E, 16 February 2011. ***South Island:*** NMNZ P.033548 (2, 110–133) Foul Point, Abel Tasman, 40°54' S, 173°4' E, 8 m, 3 December 1993.

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Review of the Australian endemic odontocerid genus *Barynema* and status of Australian *Marilia* (Trichoptera)

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Abstract

Wells, A. and St Clair, R.M. 2021. Review of the Australian endemic odontocerid genus *Barynema* and status of Australian *Marilia* (Trichoptera). *Memoirs of Museum Victoria* 80: 101–112.

In this review of Australian Odontoceridae, we revise details of the two established species in the endemic genus *Barynema* Banks – *B. costatum* Banks and *B. australicum* Mosely – and describe six new congeners: *B. paradoxum* sp. nov., *B. lorien* sp. nov., *B. lobatum* sp. nov., *B. dilatum* sp. nov., *B. dolabratum* sp. nov. and *B. goomburra* sp. nov. For the only other odontocerid genus recorded for Australia, *Marilia* Müller, we discuss the present status of the three described species – *M. bola* Mosely, *M. aenigmata* Neboiss and *M. fusca* Kimmins – and outline our efforts and those of others to resolve problems of species delimitation based on morphology. We select a new replacement name for *Marilia fusca* and provide brief notes on the larvae of both genera.

Keywords

venation, CO1 data, distributions, homonym

Introduction

The family Odontoceridae is one of several groups among Australian Trichoptera, upon which Arturs Neboiss (late of Museums Victoria) made some preliminary studies but then set them aside. In 2003, he published a new Tasmanian species of *Marilia* Müller, 1878 (*M. aenigmata*), thus bringing to three the Australian species reported for this genus. *Barynema* Banks, 1939, the only other odontocerid genus recorded for Australia, is endemic, comprising two established species. Discrimination between adult males of these two *Barynema* species and a further six species, newly described here, is reasonably easy based on male genitalic features, augmented for some by thoracic features, but this is not so for discrimination between adult specimens referrable to *Marilia*.

The genus *Marilia* has almost a worldwide distribution. Features of the genus are discussed in detail in works by Oláh and Johanson (2010) and Yang et al. (2017). Oláh and Johanson (2010) found that "[m]any species have similar male genitalia, and it is difficult to differentiate all species by examining the phallic apparatus alone" (p. 73). Working with east Asian species, they advocated discrimination of species based on combined genitalic features and cephalic setal wart patterns.

The three species of *Marilia* described from Australia – *Marilia bola* Mosely, 1953, and *M. fusca* Kimmins, 1953 (both described in the work by Mosely and Kimmins, 1953), and *M. aenigmata* – all have very uniform male and female genitalia. Differentiation of the first two appears, on paper, to be relatively simple. Males of *Marilia bola* have the eyes holoptic (almost touching the vertex) and a tuft of long setae on the anal lobe of the hind wing, whereas males of *M. fusca* have the eyes dichoptic (not approximated) and lack the tuft of setae on the wing. The female of *M. bola* was described and illustrated, but not the female of *M. fusca*. Neboiss, in describing the Tasmanian *M. aenigmata*, gave a small table of comparison of features of all three species, noting that *M. aenigmata* exceeds *M. bola* in size and, in comparison with *M. bola*, lacks Fork 3 in the female forewing and has hindwing Fork 1 sessile, not stalked (petiolate).

Confusing any simple separation of species, however, in preliminary studies on Australian *Marilia* specimens in the considerable Museums Victoria collection, Brian Armitage (in 1990) recognised two major sets among *Marilia* specimens from sites along the length of the Great Dividing Range, from central Victoria to far north-eastern Queensland, and labelled specimens accordingly. He designated these *Marilia* Sp. A and *Marilia* Sp. B, based mainly on wing features. In several samples from a single site, he recognised both forms. Males of both sets have the compound eyes holoptic and, in their genitalic features, exhibit no clearly consistent differences. Females are inseparable on genitalic features. Both sexes of *Marilia* Sp. B have Fork 1 in the hind wing petiolate, and the associated females have forewing Fork 3 present. Thus, *Marilia* Sp. B could be *Marilia bola*.

Armitage's Sp. A has Fork 1 in the hindwing sessile and the associated females lack forewing Fork 3. It shares these wing features and genitalic characteristics with *M. fusca* and *M. aenigmata*. However, the eyes of the type specimen of *M. fusca* as described by Kimmins (in the work by Mosely and Kimmins, 1953) are dichoptic; thus, *Marilia* sp. A is not conspecific with *M. fusca*. Or, conceivably, it could be if the situation is as Oláh and Johanson (2010) determined for their newly described South-East Asian species *Marilia malickyi* – that there is "[i] ntraspecific variation in the interocular distance" (p. 74). Armitage's Sp. A does conform morphologically with *M. aenigmata*. The body size of mainland specimens varies considerably, with many being much smaller than the Tasmanian specimens.

The only specimens in the available collections that concur completely with the description of *M. fusca* are in several small samples collected from streams in the Mount Spec State Forest (to the north of Townsville in north-east Queensland) and a stream near Tully. Surprisingly, no dichoptic males have been identified among samples from further south to the Sydney region or the Oxley Rivers region of New South Wales from whence the type and paratypes, respectively, were taken, nor further to the north in Queensland.

None of this is particularly satisfactory and does not corroborate the equally unsatisfactory preliminary results from the limited patchy and geographically scattered CO1 data from adults and larvae that are available on the Biodiversity of Life Database (BOLD; http://www.boldsystems.org). The BOLD data suggest there are at least eight species of *Marilia* in Australia, most with large genetic distances of at least 10% between them. This is apparent from the very limited number of specimens available for genetic analysis. More collecting and analysis will probably reveal further species. Three specimens from north-east Queensland, from localities from which specimens identified by Armitage as sp. B were collected, have venation that differs from both *M. aenigmata* and *M. bola*.

Similarly puzzling is the available information on larvae of Australian species of *Marilia*. Larvae and pupae from the Yarra River at Reefton, Victoria, were described by Drecktrah (1990) as those of *M. fusca*. He gave no indication of how the identification was made, and it is impossible to be certain from the anterior view if the pupal head illustrated by Drecktrah would have emerged as female or male, holoptic or dichoptic. It now seems very unlikely that the larvae described by Drecktrah are *M. fusca*. In 2004, Dean et al. published a key for discrimination of late instar larvae of *Barynema* and *Marilia*, and separation of three species of *Marilia*, identified as *M. bola*, *M. fusca* and *M. aenigmata*; photographic images are given to illustrate diagnostic features used in the key. *Marilia fusca* and *M. aenigmata* were separated in the key simply by geography, and the authors comment that their larvae are similar and may eventually be found to be the same species. In recent collecting of *Marilia* larvae from New South Wales and Queensland, St Clair (unpublished) has noticed further small differences. Identification of larvae of *Marilia* species is therefore not possible until larvae can be associated with known adults. All available specimens can be assigned to two larval types that align with the names given by Dean et al. (2004). These are probably better labelled "*Marilia* larval sp. 1" (was *bola*) and "*Marilia* larval sp. 2" (was *fusca*) since such confusion is now recognised. Further studies involving association of adults and close morphological examination of larvae are required.

Marilia fusca is a junior secondary homonym of the name *Anisocentropus fuscus* Banks, 1905 (synonymised with *Marilia flexuosa* Ulmer, 1905, by Betten, 1934), so here we select a replacement name.

Overall this is a confusing mix, probably only solved by a thorough and comprehensive combined morphological and molecular phylogenetic study. For the present, it is not possible to assign Australian specimens of *Marilia* to species. Thus, we can offer no further insight into Australian *Marilia*. The late Arturs Neboiss would understand.

Material and Methods

Most of the material studied is in the collection of Museums Victoria, Melbourne (NMV) and bears the standard NMV registration number. Genitalic specimens that were macerated and cleared by Neboiss are tagged with PT-numbers and several others have WTH (Wet Tropics Heritage) numbers or BOLD identifications. A small number of specimens are in the Australian National Insect Collection (ANIC), Canberra, or will be lodged in the Queensland Museum (QM). Images of types in the Natural History Museum, London (BMNH) were provided by Dr Ben Price. Other images were taken at ANIC by AW and were prepared using a stereomicroscope linked to a Leica Application Suite (version 4.2) to integrate multiple images; some of the images are of cleared, others of intact, specimens. Plates were prepared in Adobe Photoshop (version 12).

The terms applied to wings follow Mosely and Kimmins (1953), and the terms applied to genitalic structures follow Yang et al. (2017), save for structures that in ventral view appear beside the phallus, for which we follow Mosely and Kimmins in using the term "upper penis cover". This latter structure could represent tergite X or the phallobase, but it appears to arise further ventrad than one would expect for the former and to be independent of the phallus, so probably is not homologous with the latter.

Taxonomy

Marilia Müller

Marilia fusca Kimmins (in the work by Mosely and Kimmins), 1953: 167, fig. 112.

Marilia disjuncta nom. nov., new replacement name for *Marilia fusca* Kimmins, preoccupied by *Anisocentropus fuscus* Banks, 1905, a junior synonym of *Marilia flexuosa* Ulmer, 1905.

Barynema Banks

Figures 1–35

Barynema Banks 1939: 483, type species: *Barynema costatum* Banks, 1939 by monotypy.

In their treatment of the Australian endemic genus *Barynema*, Mosely and Kimmins (1953) discussed its early placement in the family Calamoceratidae and their rationale for transferring the genus to the family Odontoceridae on the grounds that *Barynema* lacks the median cell in the forewing. Adults of *Barynema* species are distinguished from Australian representatives of *Marilia* by having a pair of setose warts on the mesoscutum, whereas *Marilia* has two rows of setae; males of many specimens of *Marilia* have holoptic compound eyes, not seen in any *Barynema*. Two species of *Barynema* – *B. australicum* Mosely, 1953, and *B. goomburra* sp. nov. – also have a pair of setate warts posteriorly on the mesoscutellum, a characteristic that appears to be absent in all other Odontoceridae. This could be considered a distinguishing feature at the genus level but given the very close similarity of other male and female features of species assigned to *Barynema*, we believe all eight species are appropriately referred to a single genus. Similar variation in presence and absence of mesoscutal and mesoscutellar setal warts and their arrangement is seen in the closely related Philorheithridae (Neboiss, 1977).

In the inferior appendages of the males of some species of *Barynema* (e.g. *B. costatum* and *B. australicum*), the harpago appears to be fused with the coxopodite (or lost?). In other species, a rather similar structure (when viewed laterally) appears to be simply an extension of the coxopodite that is probably homologous with the structure termed "subapicodorsal lobe of an inferior appendage" by Yang et al. (2017, p. 88). The socketed harpago forms a smaller, but morphologically similar, structure (e.g. *B. lobatum* sp. nov.) or is reduced to a small triangular (*B. dilatum* sp. nov.) or subquadrate (*B. dolabratum* sp. nov.) lobe laterad of the extended coxopodite; it usually bears an area of short peg-like black setae. A similar situation appears to occur in the east Asian species *Psilotreta malickyi* Oláh and Johanson, 2010, although in that species the reduced harpago is a mesal structure. In females of *Barynema*, the apical lobes are stout structures on abdominal segment X, while in *Marilia* they are absent or fused with tergite X.

Here, new records and images are given for each of the two established species of *Barynema*: *B. costatum* from Victoria and *B. australicum* from north-eastern New South Wales. Thoracic and female genitalic features are described and illustrated for these species. In addition, six new species are described, based on male and female thoracic and genitalic features, and a key is provided for the genus. The genus has been collected along the Great Dividing Range of eastern Australia but has not been recorded further west; in the south, the genus is not recorded from west of the central ranges of Victoria or from Tasmania. Genetic data from BOLD suggest that additional species are present in Australia.

Larvae of a few species can be associated with the adult using the CO1 barcode. The larvae show subtle differences that may enable species separation, but this is best left until more species are associated. The larval and pupal descriptions of *Barynema costatum* by Cartwright and Dean (1987) may not be that species and may not be adequate to separate larvae of related species.

Key to males of *Barynema* Banks.

1. Mesoscutellum subcircular to rectangular, bearing small paired setate warts separate from each other and close to posterior margin (figs 29, 33) 2
- Mesoscutellum ovoid, with large paired setate warts fused and covering most of mesoscutellum (fig. 5) 3
2. Inferior appendages, each with harpago in ventral view bearing abbreviated area of short stout black peg-like setae subapicomesally; coxopodite with short mesal lobe bearing similar, but tapered, setae (fig. 32) ..... *B. australicum* Mosely
- Inferior appendages, each with harpago in ventral view bearing elongate area of short stout black peg-like setae subapicomesally; coxopodite without mesal lobe (fig. 35) ..... *B. goomburra* sp. nov.
3. Inferior appendages, each with brush of short, stout black setae on harpago subapicomesal, elongate, extending along distal half of mesal margin (figs 3, 6) ..... *B. costatum* Banks
- Inferior appendages, each with brush of short stout black setae on harpago apical and rounded, not elongate (figs 9, 13, 18, 21, 25) 4
4. Lobes of upper penis cover in ventral view expanded apicolaterally (figs 21, 25) 5
- Lobes of upper penis cover in ventral view tapered, acuminate to rounded apically, but not expanded apicolaterally (figs 9, 13, 15, 18) 6
5. Apicolateral lobes of upper penis cover in ventral view rounded (fig. 21) ..... *B. dilatum* sp. nov.
- Apicolateral lobes of upper penis cover in ventral view sharply triangular, pick-shaped (fig. 25) ..... *B. dolabratum* sp. nov.
6. Inferior appendages, each with coxopodite in ventral view about 2 times as long as wide (figs 13, 15) ..... *B. lorien* sp. nov.
- Inferior appendages each with coxopodite in ventral view subquadrate (figs 9, 18) 7
7. Coxopodites in ventral view, each with mesal margin rounded (fig. 18) ..... *B. lobatum* sp. nov.
- Coxopodites in ventral view, each with mesal margin angled obliquely from base (fig. 9) ..... *B. paradoxum* sp. nov.

Barynema costatum Banks

Figures 1, 3–8

Barynema costatum Banks, 1939: 484, figs 43, 51, 54.

Material examined. Holotype. male, Victoria, Mount Donna Buang, 6–7 December, Darlington (ANIC, ex CZM, dry on a pin). Victoria: 1 male (dissected), Cement Creek near Warburton, 4.xi.1972, P. Zwick (NMV Tri-26514, PT-1389). Victoria: 1 adult female, same data (NMV Tri-26517, PT 1890); 1 male (pharate adult, dissected), small trib. Snobs Creek, Snobs Road crossing bridge, 11.6 km u/s Eildon Road, 31.x.1981, J. Dean (NMV Tri-26506); 1 female (reared), Back Creek, 1 km NE of Noorinbee, 13.x.1982, A. Bolton, reared (NMV Tri-26518).

Diagnosis. Males, when freshly caught or dried, have on the black forewing a band of white and golden hairs angled across the wing at about 3/5 length and a streak of golden scales and hairs between A1 and Cu2; on the inferior appendages, a rather elongate hairbrush-like cluster of short and blunt black setae line the inner subapical or apical region of the harpago, features that distinguish them from *B. paradoxum* sp. nov. with similar black wings, but with the distal band of hair on the forewing wing only slightly curved and the harpago with a rounded cluster of short black setae apically; in ventral view, the basal section of the coxopodite is broadly subrectangular in *B. costatum*, but more rounded in *B. paradoxum*, and the upper penis cover with each lobe expanded laterally toward the apex, rather than tapered or rounded.

Description (revised after Mosely and Kimmins, 1953).

Mesothorax with scutellum subquadrate, without mesoscutellar setate warts.

Male. Body and wings (figs 1, 3, 4) black, forewings each with gold band along proximal section of A1 and white band across vein anastomoses at about 3/5 wing length; length of each forewing 9.5 mm (n = 1). Mesoscutellum ovoid, without setate warts. Abdominal sternite VII bearing median subquadrate lobe. Genitalia: Pre-anal appendages in dorsal view stoutly conical, about length of inferior appendages; upper penis cover elongate, wrapped lateroventrad of phallus, flared and widest towards apex; inferior appendages in ventral view with coxopodite stout, subquadrate basally; harpago in ventral view slender, with elongate apicomesal brush of sharp, stout black setae lining distal half, giving hairbrush-like appearance.

Female. Terminalia: Distal abdomen bearing pair of short, stout, apically truncate apical lobes; striated plates ventrally on segment IX.

Distribution. Found in central and eastern Victoria.

Remarks. Very few specimens of *B. costatum* have been collected – many of the specimens previously identified as *B. costatum* are assigned here to the new species *Barynema paradoxum* sp. nov. BOLD data groups the two, with only a short distance between them. One of the few confirmed *B. costatum* specimens is a pharate pupa from a tributary of Snobs Creek on the north-western edge of the Great Dividing Range in central Victoria, images of which are included here (figs 5–8), particularly to show the form of the mesoscutellum that is obscured by the pin on the dried type.

Barynema paradoxum sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:62A5E978-BCFE-49A3-829D-4F08FB542881

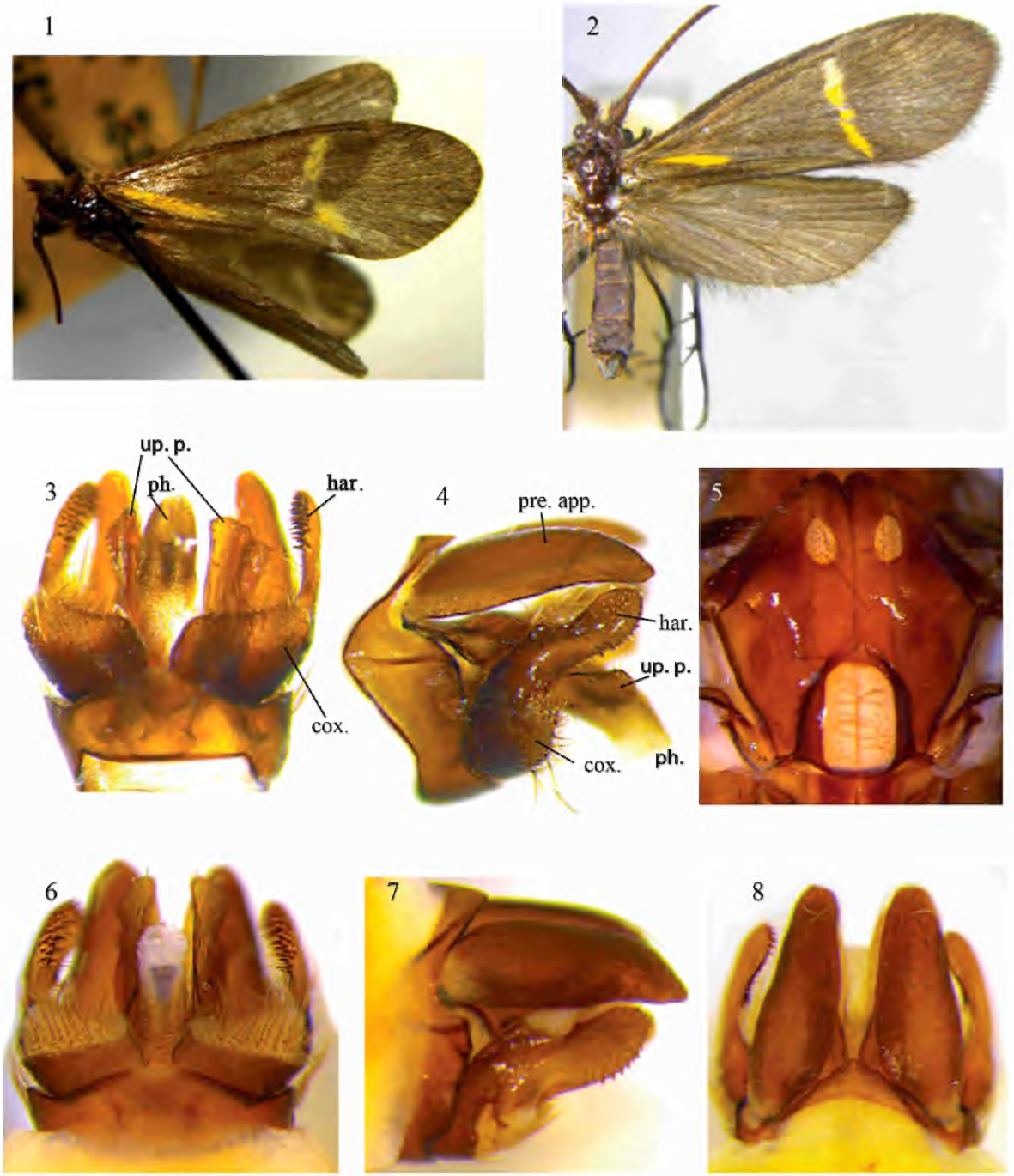
Figures 2, 9–12

Material examined. Holotype. male, New South Wales, 8 km N of Nowra, 21.x.1966, N.D. (NMV Tri-27118, PT-1646).

Paratypes. New South Wales: 2 males, data as for holotype, 21.x.1966, N.D. (NMV Tri-27113); 4 males, data as for holotype, 21.x.1966, N.D. (NMV Tri-27115); 1 male, Minnamurra Falls, N of Kiama, 25.iii.1973, A. Neboiss (NMV Tri-27114); 2 males, Mumbulla Creek, near Bega, 20.xi.1978, I. Campbell (NMV Tri-27110); 3 males, 1 female, Minnamurra Falls, 22.x.1982, G. Theischinger (NMV Tri-27139); 2 males, Bundanoon, 34° 39' S 150° 18' E, ix.1983, G. Theischinger (NMV Tri-27137).

Other material. New South Wales: 1 male [pinned], Brown Mountain, 2.xii.1956, E.F. Riek (ANIC); 2 males [pinned], Macquarie Falls, 14.ix.1960, D.H. Colless (ANIC); 3 males [pinned], upper Kangaroo Valley, 24.ix.1960, E.F. Riek (ANIC); 1 male, eastern Fall, Clyde Mountain, 26.x.1960, E.F. Riek (ANIC); 2 males, 1 female, Minnamurra Falls, 23.x.1962, D.K. McAlpine (NMV Tri-27062; 2 males, 1 female, Minnamurra Falls (NMV TRI-27062); 1 male, 1 female, New South Wales, Macquarie Pass, 13x.1986, "G. Thei. & L. Mu." [G. Theischinger and L. Muller] (NMV Tri-27133); 1 male, New South Wales, Macquarie Rivulet, W of Shell Harbour, 34° 34' S 150° 41' E. 4.i.1990, G. Theischinger (NMV Tri-27134); 1 male, same data (NMV Tri-27070); 1 male, Bundanoon, Fairy Bower, 35° 39' S 150° 18' E, ix.1991, G. Theischinger (NMV Tri-27135); 2 male, same data (NMV TRI-27137); 1 male, same data (NMV TRI-27138); 1 female, New South Wales, Yadboro Creek, Budawang Range, 40 km SW of Nowra, 35° 22' S 150° 03' E, xi.1991, G. Theischinger (NMV Tri-27136); 1 female, Yadboro Creek, Budawang Range, 40 km SW of Nowra, xi.1991, G Theischinger, 35° 22' S 150° 03' E (NMV TRI-27136); 1 male, South East Forests National Park, trail near Monaro Highway, malaise in Hopping Joe Creek, 37° 12' 58" S 149° 18' 37" E, 5.xii.2004–12.i.2005, C. Lambkin, N. Starick (ANIC); 16 males 1 female, East Boyd State Forest, Anteaters Road, 55 km SE Bombala Forest, 37° 12' 18" S 149° 42' 24" E, 6.xii.2004–12.i.2005, C. Lambkin, N. Starick (ANIC); 1 male, New South Wales, Polblue Creek, Barrington Tops Forest Road, 31° 57' S 151° 26' E, 2.xii.2007, A. Glaister, J. Dean and R. St Clair (NMV Tri-54560); 1 male, tributary of Macquarie Rivulet off Clover Hill Road, 29.ix.2017, Z. Billingham (NMV Ento 2018-246, JOS-424); 1 male, Minnamurra Creek, off Minnamurra Rainforest Walk, 3.x.2017, Z. Billingham (NMV Ento 2018-246, JOS-423); 13 males, 1 female, Budawang National Park, Mount Budawang Road, 35.4563 S 149.4455 E, 16.i.2019, K.M. Bayliss, J. Lumbers and D.K. Yeates (ANIC). Victoria: Coopracambra National Park, malaise trap over Beeline Creek, 27 km NNE of Cann River, 5.xii.2004–12.i.2005, C. Lambkin, N. Starick (ANIC).

Diagnosis. Males of *Barynema paradoxum* resemble those of *B. costatum* in having distinctive black wings with a median white band across the area of vein anastomoses and a band of bright yellow hairs between veins Cu2 and A1. But in *B. paradoxum*, the white band is slightly curved, not angled, and the area of golden setae is smaller. Like *B. costatum*, *B. paradoxum* shares with *B. dilatum* sp. nov., *B. lorien* sp. nov. and *B. dolabratum* sp. nov. the absence of setate warts on the mesoscutellum and, as with those three species, the male of this new species has a rounded club of short, stout black setae apically on the distal extremity of each inferior appendage, not an elongate brush as in *B. costatum*. Together with *B. lorien*

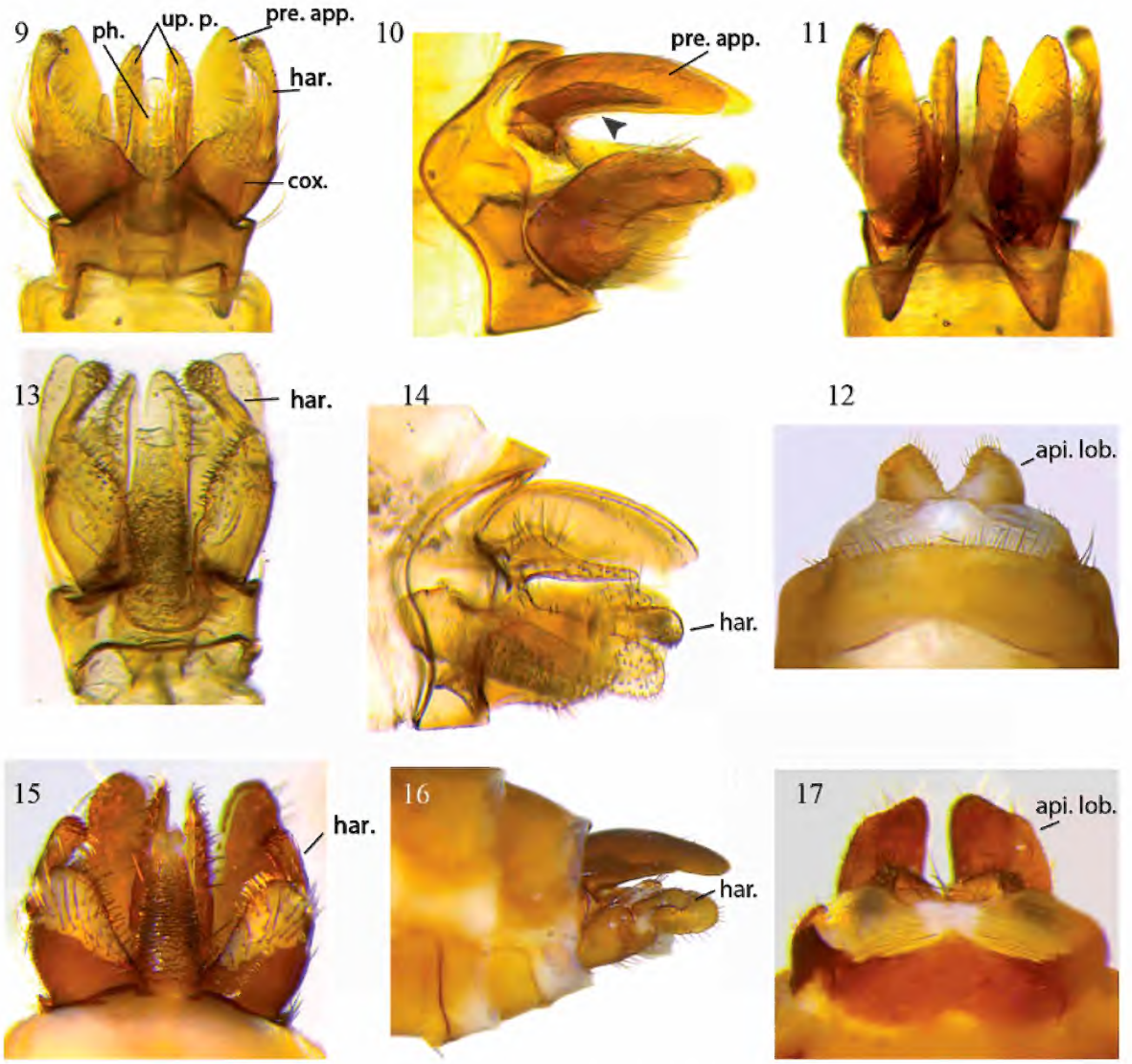


Figures 1–8, *Barynema* species. 1, 3, 4, *Barynema costatum* Banks holotype male: 1, body and wings, dorsal; 3, 4, genitalia, ventral and lateral, respectively. 2, *B. paradoxum* sp. nov., New South Wales, Upper Kangaroo Valley, body and wings, dorsal; 5–8, *B. costatum*, male, Victoria, tributary of Snobs Creek (NMV TRI-27406): 5, mesothorax, dorsal; 6–8, genitalia, ventral, lateral, and dorsal, respectively.
Abbreviations: cox. = coxopodite; har. = harpago; ph. = phallus; pre. app. = pre-anal appendages; up. p. = upper penis cover.

and *B. lobatum* sp. nov., *B. paradoxum* has the ventrolateral lobes of the upper penis cover tapered apically, rather than expanded. *Barynema paradoxum* is characterised by the coxopodite of each male inferior appendage subquadrate, not longer than wide in ventral view and not produced to form a rounded lobe at its apicomesal angle.

Description. Mesothorax without mesoscutellar setate warts. Body and wings black, each forewing with slightly curved band of white setae across vein anastomoses.

Male. Length of each forewing 6.2–9.7 mm (n = 10). Abdominal segment VII bearing small, sharp, sclerotised median spur. Genitalia: Pre-anal appendages stout, apices



Figures 9–17, *Barynema* species. 9–12, *B. paradoxum* sp. nov., holotype, New South Wales, Nowra (NMV TRI 27118, PT-1646): 9–11, male genitalia, ventral, lateral, and dorsal, respectively; 12, female, New South Wales, Yadboro Creek, Budawang Range, 40 km SW of Nowra (NMV TRI-27136) terminalia, ventral. 13–17, *B. lorien* sp. nov.: 13, 14, holotype male, New South Wales, Lansdowne via Taree (NMV TRI-27061, PT-1564), genitalia ventral and lateral, respectively; 15, 16, paratype male, Queensland, Lamington National Park (NMV TRI-27061), genitalia, ventral and lateral, respectively; 17, paratype female (NMV TRI-27061), terminalia, ventral.
Abbreviations: api. lob. = apical lobe; cox. = coxopodite; har. = harpago; ph., phallus; pre. app. = pre-anal appendages; up. p. = upper penis cover.

narrowly rounded in dorsal view; lobes of upper penis cover in ventral view tapered to acuminate apices; inferior appendages, each with coxopodite in ventral view stout, subquadrate basally, harpago about length of coxopodite, slender with a cluster of short, bristle-like dark setae on rounded club-shaped apex.

Female. Length of each forewing 9.0 mm (n = 1). Terminalia: Distal abdomen bearing pair of short apical lobes, stout basally, rounded laterally and tapered to rounded apices; striated plates ventrally on segment IX.

Distribution. Widespread in eastern New South Wales, extending into far eastern Victoria, possibly overlapping with *B. costatum*.

Etymology. Named for the past confusion over this species, and the paradox presented by the variability in male genitalic structures. Most specimens were identified previously as *B. costatum*.

***Barynema lorien* sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:E8CB61B0-BA99-4CC9-8A92-E94F3037E18D

Figures 13–17

Material examined. Holotype. male, New South Wales, Lansdowne via Taree, 29.ix.1985, G.W. Williams (NMV TRI-27071, PT-1564)

Paratypes. Queensland: 2 males, 1 female, [Lamington] National Park, 1.xi.1954, T.E Woodward (NMV TRI-27060); 1 male, Lamington National Park, 15.xi.1955, Yeo (NMV TRI-27069); 1 male (reared from pupa), Tamborine Mountain, iii.1962, K. Korboot (NMV TRI-27068); 1 female (reared from pupa), same data (NMV TRI-27067); 3 males, 1 female, Lamington National Park, xi.1982, T. Hinger (NMV TRI-27061); 1 male, Lamington National Park, xi.1982, G. Theischinger (NMV TRI-27065).

Other material. New South Wales: 1 male 1 female, Wentworth Falls, 22.xi.1960, C.N. Smithers (NMV TRI-27059); 1 male, same data (NMV TRI-27070); 1 male, [Barrington Tops State Forest], Manning River, Pheasant Creek Road, 3.xii.2007, A. Glaister, J. Dean and R. St Clair (NMV TRI-54568, JOS-237).

Diagnosis. Resembling *B. paradoxum*, *B. costatum*, and *B. lobatum* sp. nov. in having males with the pre-anal appendages stout, apically rounded. The male differs from that of *B. costatum* in having each inferior appendage terminating in a small rounded area of short black setae, not an elongate brush. It is distinguished from *B. costatum* by having the lobes of the upper penis cover in ventral view acute apically, not flared distally as in *B. costatum*, and is distinguished from *B. paradoxum* by having the basal region of each inferior appendage subrectangular, not subquadrate, and from *B. lobatum* sp. nov. which has the mesal angle more strongly produced, rounded. Females resemble those of *B. lobatum*, having the apical lobes short, stout, and stepped (obliquely truncate).

Description. Mesothorax without mesoscutellar setate warts.

Male. Length of each forewing 6.8–7.5 mm (n = 4). Abdomen with small sharply pointed spur medially on sternite VII. Genitalia: Pre-anal appendages stout, rounded apically. Upper penis cover forming pair of elongate lobes of more or less uniform width for most of length, tapered slightly to apex. Inferior appendages each with coxopodite basally long, subrectangular to ovoid in ventral view, without any tufts of setae or mesal lobes, harpago slender at base, slightly dilated distally, with round pad of short, stout black setae apically.

Female. Length of each forewing 8.3–9.6 mm (n = 3). Terminalia: Apical lobes, slightly stepped toward rounded apices.

Distribution. Found from eastern New South Wales, from the Blue Mountains to the west of Sydney to south-eastern Queensland.

Etymology. Named after the Lorien Wildlife Refuge and Conservation Area near Lansdowne, New South Wales.

***Barynema lobatum* sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:5985E223-FC68-48B4-A1C4-19D51BD5E0C2

Figures 18–20

Material examined. *Holotype.* male, Queensland, Montville, Bon Accord Falls, 27.ix.1955, A.N. Burns (NMV Tri-27064).

Paratypes. Queensland: 3 male, 1 female, Montville, Bon Accord Falls, 29.ix.1955 A. N. Burns (NMV TRI-27063); 1 male, same data (NMV Tri-27066); 1 male, south-east Queensland, Stony Creek, Conondale Range, 10.viii.1988, S. Bunn (NMV Tri-27120).

Diagnosis. In most features, *B. lobatum* sp. nov. resembles *B. lorien* sp. nov. but alone among congeners, this species has the apicomesal angle of the otherwise subquadrate coxopodite of the inferior appendages produced and rounded distally; the pre-anal appendages are tapered distally, and a small rounded mesal process occurs on sternite VII. The female is indistinguishable from those of *B. lorien*, both having stepped (obliquely truncate) apical lobes.

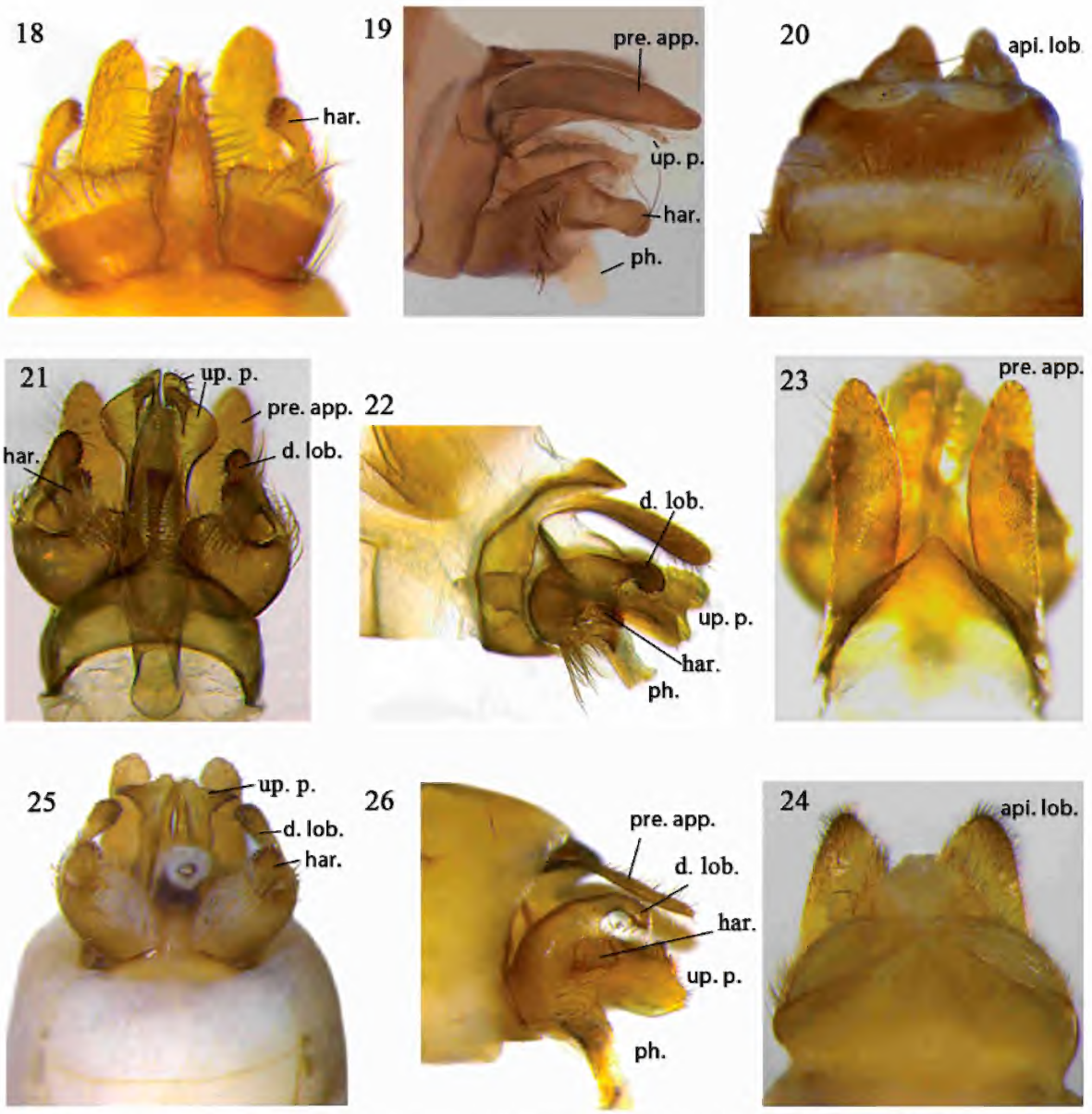
Description. Thorax with mesoscutellum almost subquadrate, pale, margin dark, lacking setate warts.

Male. Length of each forewing 5.2–7.2 mm (n = 5). Sternite VII with small, apically rounded median tab. Genitalia: Pre-anal appendages stout in dorsal view, tapered to rounded apices, in lateral view almost same width throughout, apically rounded. Lobes of upper penis cover in ventral view constricted distally to form sharp tips, in lateral view stout, rounded apically. Inferior appendages each with coxopodite in ventral view stout, apicomesal angle slightly produced, rounded; harpago narrow near base, cluster of short, dark, bristle-like setae apically.

Female. Length of each forewing 8.6 mm (n = 1). Terminalia: Distal abdomen bearing pair of apical lobes, stout basally, narrowed laterally, and produced to rounded apex.

Distribution. Known only from north of Brisbane in the Sunshine Coast region of south-eastern Queensland.

Etymology. Named for the expanded apicomesal angles of the inferior appendages.



Figures 18–26, *Barynema* species. 18–20, *B. lobatum* sp. nov.: 18, holotype male, Queensland, Montville, 27.ix.1955, (NMV Tri-27064), genitalia ventral; 19, paratype male (NMV 27120), lateral; 20, paratype female (NMV TRI-27063) terminalia, ventral. 21–24, *B. dilatum* sp. nov.: 21–23, holotype, male (NMV WTH-2966, PT-2033) genitalia ventral, lateral, and dorsal, respectively; 24, paratype female (Python Creek NMV), terminalia, ventral. 25, 26, *B. dolabratum* sp. nov. holotype male, (Oliver Creek NMV), genitalia, ventral and lateral, respectively.
Abbreviations: api. lob. = apical lobe; d. lob. = dorsal lobe of inferior appendages; har. = harpago; ph. = phallus; pre. app. = pre-anal appendages; up. p. = upper penis cover.

***Barynema dilatum* sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:26539E9C-AFA3-4F1B-BD16-B4C2F76A38E8

Figures 21–24

Material examined. Holotype. male, north Queensland, Carron Creek, Kirrama State Forest, April 1993, G. Theischinger, 18° 06' S 145° 41' E (NMV WTH-2966 PT-2033).

Paratypes. North Queensland: 5 males, Carron Creek, Kirrama State For., 17° 50' S 145° 35' E, April 1993 (NMV WTH-1171); 5 males, same data (NMV WTH-1174); 5 males, same data (NMV WTH-1172); 5 males, same data (NMV WTH-1173); 5 males, same data (NMV WTH-1174); 5 males, same data (NMV WTH-1175); 5 males, same data (NMV WTH-1176); 3 males, same data (NMV WTH-1345); 7 males, north Queensland, Goodard Creek, Kirrama State Forest, April 1993, G. Theischinger, 18° 06' S 145° 41' E (NMV WTH-1040); 7 males, same data (NMV WTH-1041); 17 males, 6 females, stream on Tully Gorge Road, 6.7 km d's of power station, M. Shackleton and J. Mynott, 8.v.2011 (NMV Tri-54556).

Other material. North Queensland: 3 females, upper Mulgrave River via Gordonvale, 29–30 April 1970, S.R. Curtis (NMV WTH-0786); 5 male, same data (WTH-2654); 1 female, Lock-Davies Creek Road, Lamb Range, Mareeba District, 10 November 1974, M.S. Moulds (WTH-0437 PT-2028); 1 female, upper Freshwater Creek, Whitfield Range, Cairns, 24 August 1974, MV-light, MS Moulds (WTH-0615); 1 male, same data (NMV WTH-0603); 1 male, same data (NMV WTH-0604); 1 male, upper Freshwater Creek, Whitfield Range, near Cairns, 15 December 1974, MS Moulds (NMV WTH-0606); 1 male, 1 male, same data (NMV WTH-0605); 1 male, same data (NMV WTH-0607); 2 females, same data (NMV WTH-0614); 1 male, the Crater, near Herberton, 18 December 1974, M.S. Moulds (NMV WTH-0602); 1 female, Mareeba, Davies Creek Road, 21 January 1976, Walford-Huggins (NMV WTH-0616); 1 male, State Forest, 24 km along Goldsborough Road near Gordonvale, 27.xii.1980, M.S. and B.J. Moulds (NMV WTH-1350); 1 male, Behana Gorge, Cairns, 16 November 1982, T. Hinger, 17° 11' S 145° 50' E (NMV WTH-0608); 2 females, same data (NMV WTH-0609); 1 male, Mossman Gorge, Daintree National Park, 17 November 1988, MV lt, K. Walker (NMV WTH-0598); 1 male, river on Lake Morris Road, Cairns, 3.v.2011, 16.9412 145.71762 (NMV EPAVT122); 2 males, 5 females, river on Lake Morris Road, Cairns, 16.9412 145.71762, 3.v.2011, J. Mynott and M. Shackleton (NMV Tri-54557); 1 male, small creek beside Josephine Falls, M. Shackleton and J. Mynott, 6.v.2011 (NMV Tri-54559); 1 male, 1 female, Josephine Falls, 17.4338 145.8630, Shackleton and Mynott 110506-7, 6.v.2011 (NMV Tri-54558); 3 males, Dunn? Creek at Bridge 11, Kirrama Range Rd, ~14 km from national park sign, –18.2138 S 145.7982 E, 24.x.2017, D. Cartwright and R. St Clair; 1 male, Mulgrave Road, Goldsborough Valley Campsite, Wooroornoonan National Park, 17.2374 S 145.7733 E, 26.x.2017 (NMV JOS 451); 1 male, Python Creek in Tully Gorge Road, ~52 km NW of Tully, 17.7662S 145.5895E, 2 November 2017, D. Cartwright and R. St Clair (QM JOS-448).

Diagnosis. The male of *Barynema dilatum* closely resembles that of *B. dolabratum* sp. nov. in having the inferior appendages each with the harpago reduced to a small apically setose ventral lobe and the coxopodite in lateral view produced and curved ventrad distally. In *B. dolabratum*, the upper penis cover in ventral view appears to form two lobes apically, with the ventral lobe expanded and rounded laterally, in contrast with *B. dolabratum*, which has the upper penis cover in ventral view pick-shaped apically.

Description. Mesothorax with mesoscutellum shield-shaped, without setate warts; fresh adult males with body and wings dark except white area at anastomosis on wings.

Male. Length of each forewing 9.3–10.3 mm (n = 10). Sternite VII without median tab or spur. Genitalia: Pre-anal appendages in dorsal view broadest at about midpoint, constricted towards base. Upper penis cover distally bilobed, dorsal lobe tapered apically in ventral view, rounded in lateral view, ventral lobe expanded and rounded laterally towards apex. Inferior appendages each with coxopodite base short, stout, produced to form a dorsal lobe with slender neck before slightly dilated apex bearing short stubby black setae, harpago short, rod-shaped, bearing dense brush of short black setae apically.

Female. Length of each forewing 11.8–17.7 mm (n = 10). Terminalia: Apical lobes conical, tapered to darkly sclerotised apices.

Distribution. From north-eastern Queensland, west of Tully to the Cairns district.

Etymology. The name is derived from the Latin *dilato*, to extend, for the lateral swellings on the upper penis cover lobes.

***Barynema dolabratum* sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:70CBA5A9-B547-4657-9FF7-F5D89AABE20E

Figures 25, 26

Material examined. *Holotype.* male, north Queensland, Gap Creek, 10.ii.1982, M.S. Moulds (NMV WTH-0599, PT-1176).

Paratypes. North Queensland: 1 male, Gap Creek, Mount Finlayson Range, S of Cooktown, 25 November 1974, M.S. Moulds (NMV WTH-0601); 1 male, Gap Creek, 10 February 1982, M.S. Moulds (NMV WTH-0600); 1 male, Oliver Creek on Bloomfield Road, 8 km S of Cape Tribulation, 16.1377 S 145.4408 E, 29.x.2017, D. Cartwright and R. St Clair (QM); 1 male, data as above, D. Cartwright and R. St Clair, NMV (JOS-452).

Diagnosis. This species, known only from males, closely resembles that of *B. dilatum*, but is distinguished by the slightly smaller body, darker body, mesoscutal setate warts elongate-ovoid, and the sharp, pick-shaped form of the upper penis cover lobes in ventral view.

Description. Mesothorax with mesoscutellum shield shaped, without setate warts.

Male. Length of each forewing 9.0–10.6 mm (n = 5). Small white area around lower part of wing at anastomosis. Sternite VII without median spur or tab. Genitalia: Pre-anal appendages stout, apically rounded in ventral view. Upper penis cover lobes produced distally, pick-shaped apicolaterally in ventral view, in lateral view triangular apico-dorsally. Inferior appendages each with coxopodite broad at base, in lateral view produced in slender, curved dorsal lobe bearing cluster of stubby black setae apically; harpago forming short apically truncate lobe bearing stout peg-like black setae at tip.

Female. Unknown.

Distribution. Collected from Cape York, Queensland, from the two sites to the north of Cairns and south of Cooktown.

Etymology. From the Latin *dolabratus*, meaning pick-shaped for the appearance of the upper penis cover lobes.

Barynema australicum Mosely

Barynema australicum Mosely, in Mosely and Kimmins, 1953: 162, figs 108, 109.

Figures 27–32

Material examined. Holotype. male, New South Wales, Ebor, 5.i.1916, R.J. Tillyard, (BMNH) [head and abdomen mounted in balsam, images courtesy B. Price, BMNH]

New South Wales: 1 female, Wilson River Reserve near Bellangry, 5.xii.1986, G. Theischinger (NMV TRI-26493); 1 male, Coomboodja Creek, Washford National Park, 29° 16' S 152° 22' E, 5.i.1986, Theischinger (NMV Tri-27119, PT-1655); 2 females, same data (NMV Tri- 27116); 1 male ,1 female, "Cockerawo… Creek", 23 km WNN Bellangry, 8.xii.1986, 730 m, G. Theischinger (NMV TRI-26505); 19 males 1 female, Orara West State Forest, Tuckers Knob, 29° 41' S 152° 48' E, 27.xi.1990, G. Theischinger (NMV TRI-27117); 1 male, Manning River, Pheasant Creek Road, A. Glaister, J. Dean and R. St Clair, 3.xii.2007, 31° 53' S 151° 29' E (NMV TRI-54569, JOS-238); 1 male, Never Never River, Whitneys Road, –30.33001S 152.86222E, 10. xi.2010, 10110-5, MS 747 [M. Shackleton] (NMV TRI-54570, JOS-108).

Diagnosis. Distinguished from most other species of *Barynema* by having a pair of setate warts on the mesoscutellum, a feature shared with *B. goomburra* sp. nov., from which it differs by having male genitalia in ventral view with the coxopodite of each inferior appendage subquadrate, and in both ventral and lateral views the harpago with a short, slender basal portion before the swollen terminal section that bears a broader hairbrush-shaped area of short blunt black setae, rather than an elongate toothbrush-shaped region as in *B. goomburra* sp. nov.

Description. Male. Length of each forewing 6.4–7.8 mm (n = 10). Sternite VII bearing apically rounded median tab. Genitalia: see Mosely and Kimmins, 1953: 162).

Female. Length of each forewing 8.4–10 mm (n = 3). Terminalia: Apical lobes on abdominal segment X short, broad, almost quadrate.

Distribution. Found in north-east New South Wales, in the Barrington Tops-Wauchope and mid north coast regions.

Remarks. Two specimens among those that have been sequenced for the BOLD project can be referred to *B. australicum*. Each appears in a different cluster on the current BOLD Taxon Identification Tree. This is due to either contamination of the CO1 gene or the presence of sibling species. Several more specimens are required before this can be resolved. This species, together with specimens here referred to *B. dilatum* sp. nov., show no presently resolvable relationships.

Barynema goomburra sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:3B854EDD-8AEB-4E71-903C-DEE0AEEF26EE

Figures 33–35

Material examined. Holotype. male, Queensland, Goomburra State Forest, NE of Warwick, 28° 03' S 152° 07' E, 20.i.1986, G. Theischinger (NMV TRI- 27112).

Paratypes. New South Wales: 1 male, 4 females, Styx River, Hyatt Flat, 8.xii.1998, G. Theischinger (ANIC).

Diagnosis. Adults of this species closely resemble those of *B. australicum* in having a pair of setose warts on the mesoscutellum; the males of both species have a brush of short, blunt black setae terminally on each harpago and, in lateral view, the pre-anal appendages are broad-based and gradually tapered distally. The male of *B. goomburra* is characterised by having the inferior appendages narrower than those of *B. australicum* and the coxopodites lacking apicomesal clusters of setae that are present in *B. australicum*. The male of *B. goomburra* resembles that of *B. costatum* with the harpago bearing an elongate and narrow brush of stout black setae occupying almost its entire inner distal margin, but differs from *B. costatum* in that *B. goomburra* has a subcircular to rectangular mesoscutellum bearing small paired setate warts separate from each other and close to the posterior margin, whereas the mesoscutellum of *B. costatum* is ovoid and with large paired setate warts fused and covering most of the mesoscutellum.

Description. Mesothorax with mesoscutellum bearing pair of setate warts close to distal margin.

Male. Length of each forewing 6.5–7.2 mm (n = 2). Abdominal segment VII bearing stoutly rounded midventral tab. Genitalia: Pre-anal appendages in lateral view elongate triangular; upper penis cover in ventral view forming pair of short, stout, apically expanded structures; inferior appendages in ventral view each with coxopodite about equal width throughout length, without apicomesal brush of setae, harpago not clearly delineated, with somewhat stout, short, blunt black setae lining entire mesal side, giving toothbrush-like appearance.

Female. Length of each forewing 8.0–9.6 mm (n = 4). Terminalia: Apical lobes broad-based, arising close to each other, then tapered to narrowly rounded apices.

Distribution. Collected from just north of the New South Wales–Queensland border, and from the Styx River in the Northern Tablelands area of New South Wales.

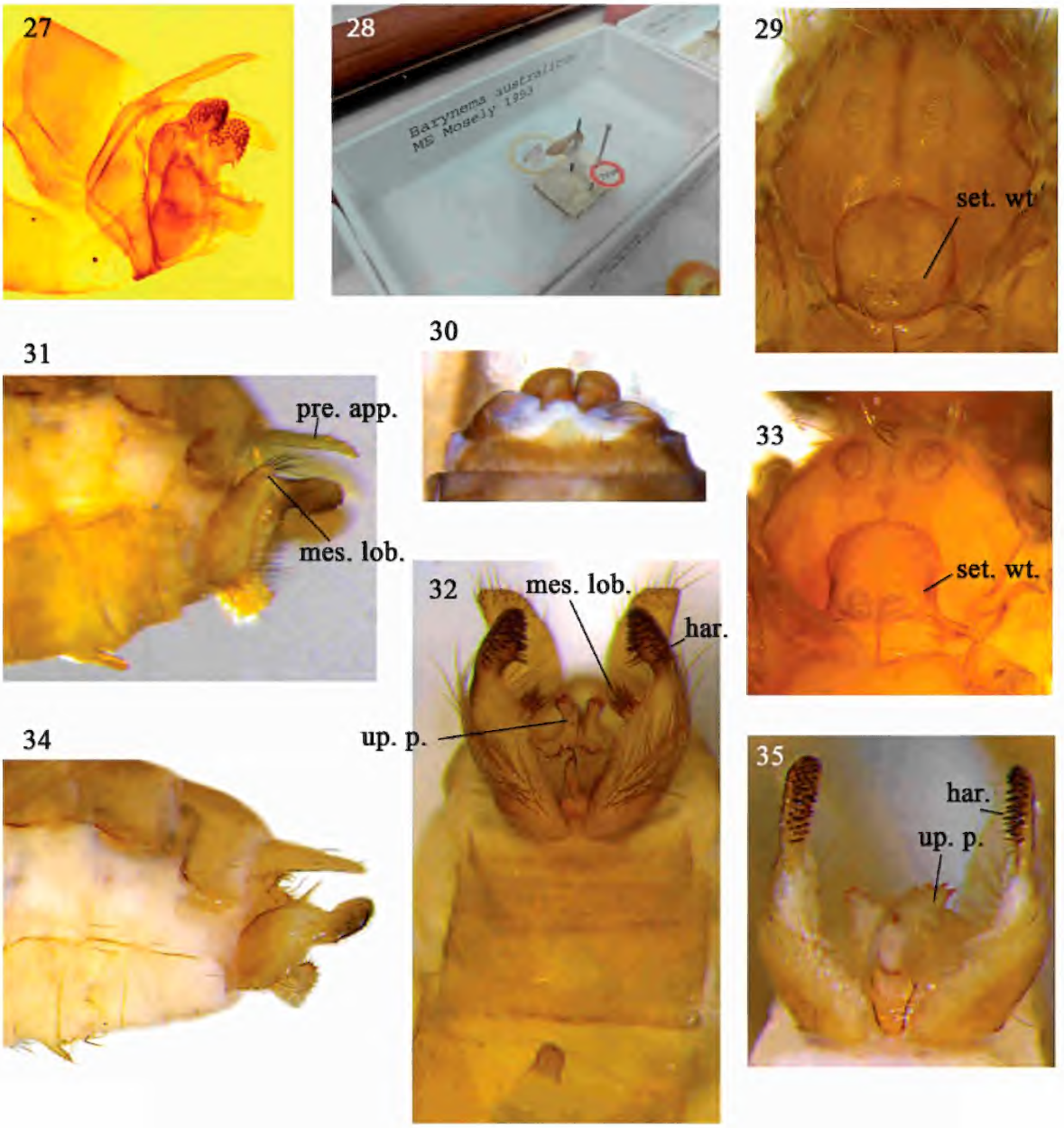
Remarks. No specimens recognisable as *B. goomburra* are among material for which molecular (CO1) data are available at present.

Etymology. Named for the holotype locality.

Acknowledgements

We thank, particularly, staff of Museums Victoria Entomology section for making both of us welcome, for making available their extensive odontocerid collection and for providing laboratory space to RSC. The Australian National Insect Collection, CSIRO, Canberra, is thanked for providing laboratory facilities for AW. Dr Ben Price, Natural History Museum, London, kindly supplied images of the type of *Barynema australicum*.

Material from Queensland collected by Michael Shackleton was taken under collecting permits WITK1027111 and that collected by David Cartwright and Ros St Clair under the Entomological Society of Queensland collecting permits WITK15549915 and TWB/02/2015. Material from New South



Figures 27–35, *Barynema* species. 27, 28, *B. australicum* Mosely, holotype male (BMNH): 27, genitalia, lateral (on microscope slide); 28, part of body and wings of holotype (images, courtesy B. Price, BMNH). 29–32, *B. australicum*, New South Wales, Orara West State Forest (NMV-27117): 29, male mesothorax dorsal; 30, female, terminalia ventral; 31, 32, male, genitalia, lateral and ventral, respectively. 33–35, *B. goomburra* sp. nov., holotype male, Queensland, Goomburra State Forest, NE of Warwick (NMV TRI-27112): 33, mesothorax dorsal; 34, 35, genitalia lateral and ventral, respectively.

Abbreviations: har. = harpago; mes. lob. = mesal lobe of coxopodite; pre. app. = pre-anal appendages; set. wt. = setate warts on mesoscutellum; up. p. = upper penis cover.

Wales was collected by Michael Shackleton under Scientific Research Permit P07/0095 and National Parks Service Scientific License S12404; by Alena Glaister, Ros St Clair, and John Dean under Scientific Research Permit P07/0095-1.0, and National Parks Service Scientific License S12404; and by Zac Billingham as bycatch under National Parks Service Scientific License SL101930.

Material from Queensland was collected under Scientific Research Permit numbers WITK06190909 (May 2010) and WITK10277111 (8 Nov 2011–7 Nov 2013). Material from Victoria was collected under Scientific Research Permits 10005961 (19 Aug 2012–31 Aug 2013).

Material from Queensland was collected under Scientific Research Permit numbers WITK06190909 (May 2010) and WITK10277111 (8 Nov 2011–7 Nov 2013). Material from Victoria was collected under Scientific Research Permits 10005961 (19 Aug 2012–31 Aug 2013).

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New species of squat lobsters of the genus *Munida* from Australia

(http://zoobank.org/urn:lsid:zoobank.org:pub:EA21667A-77A5-411D-9C1A-23ECFFF3D505)

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Abstract

McCallum, A.W., Ahyong, S.T. and Andreakis, N. 2021. New species of squat lobsters of the genus *Munida* from Australia. *Memoirs of Museum Victoria* 80: 113–152.

This study reports on new squat lobsters of the genus *Munida* collected during recent surveys of Australia's continental margins. We report on 33 species of *Munida* including seven new species and 14 new range extensions for Australia. More than 500 specimens were collected, mostly from the western continental margin of Australia, but also including a new species from deep water (>2000 m) off Tasmania. We provide new data on the colour patterns of some species and include molecular data from two mitochondrial markers (16S rRNA and COI) to support the taxonomic status of the new species.

Introduction

Australia has a vast marine realm, the third largest jurisdiction in the world, encompassing tropical and temperate biomes and connected to the highly biodiverse Indo-West Pacific region. Over the last decade, efforts to document the biodiversity of Australia's deep seafloor habitats have grown, as a system of Marine National Parks were established and monitored. Sampling of Australia's deep seafloor has revealed a high proportion of new species and significant range extensions, but most of these records await detailed taxonomic description.

Squat lobsters (Chirostyloidea and Galatheoidea) are among the most diverse groups of decapod crustaceans in deep waters, and there have been intensive efforts to describe and revise species and higher taxa from the group (Macpherson and Baba, 2011). This has been assisted by the availability of taxonomic resources such as synoptic works (e.g. Baba, 2005; Baba et al., 2008) and keys (Taylor and Poore, 2010). In addition, molecular-based approaches are helping to identify overlooked species that show only subtle morphological differences (Poore and Andreakis, 2012).

Munida is one of the largest genera of squat lobsters, currently comprising 297 species (WoRMS, 2021). The most recent major taxonomic study of *Munida* in Australia recorded 19 species (Ahyong and Poore, 2004). Additional records have since been added (e.g. Ahyong, 2007; Baba, 2005; Poore et al., 2008); so, to date, 32 species of *Munida* have been documented from Australia.

Here, we report the specimens of *Munida* collected during several deep-water surveys from 2005 to 2015, including surveys of the continental margin of Western Australia, the Great Australian Bight, Tasmanian seamounts, and the eastern Australian continental margins and abyss. We describe and illustrate new species and record new occurrences of previously described taxa. The synonymies for each species are restricted to papers published after the compilation of Baba et al. (2008). Where available, we include molecular data from two mitochondrial markers (16S and COI) to support the taxonomic status of the species.

Materials and methods

Sampling

Specimens were collected using beam trawls and epibenthic sleds in surveys aboard the FRV *Southern Surveyor* of the south-western continental margin of Australia (SS10/2005) and north-western continental margin (SS05/2007); and surveys aboard the RV *Investigator* of the Great Australian Bight (IN2015_C01_042) and the continental margin and abyss of eastern Australia (IN2017 V03). A small number of specimens were collected from south-west Tasmania (TT 01/2008) using the remotely operated vehicle Jason aboard the RV *Thomas G Thompson*. Specimens collected from well-sampled sites on Tasmanian seamounts (SS01/2008, SS02/2007) were reviewed and represent well-known species previously reported for the area; they are not redescribed herein.

Morphological methods

Specimen measurements in *Material examined* refer to postorbital carapace length (pcl), measured dorsally from the base of the rostrum (situatued at the level of the orbit) to the mid-posterior margin of the carapace, and where the rostrum is intact, carapace length (cl) is measured from the rostral apex to the mid-posterior margin of the carapace. The angle of the frontal-margin-from-the-midline is measured as the angle of the intersection between an imaginary line along the frontal margin and the median axis. Thus, a transverse margin corresponds to an angle of 90°. The lengths of articles of the cheliped are measured along the dorsal margin and those of ambulatory legs and maxilliped 3 are measured along the extensor margin and exclude spines. Abbreviations used are Mxp3, maxilliped 3; P1, pereopod 1; P2–4, pereopods 2–4; M, male; F, female; ovig., ovigerous.

Specimens are deposited in the collections of Museums Victoria, Melbourne (NMV), the Western Australian Museum (WAM), the Australian Museum, Sydney (AM), Muséum national d'Histoire naturelle, Paris (MNHN) and the South Australian Museum, Adelaide (SAM). Other abbreviations: WA, Western Australia; acq. refers to the Commonwealth Scientific and Industrial Research Organisation (CSIRO) acquisition number allocated to the specimen on board the vessel at the time of collection.

Molecular analysis

Material collected from south-western Australia (SS10/2005), being mostly preserved in formalin, was not sequenced.

Total DNA was extracted from 50–100 mg of abdominal tissue or pereopod of the target specimen preserved in ethanol following the salt-based extraction procedure described by Aljanabi and Martinez (1997) with minor modifications. The partial mitochondrial cytochrome oxidase subunit I (COI) and 16S rDNA gene (16S fragment 2) were polymerase chain reaction (PCR) amplified following primer combinations, reaction conditions and thermal cycling profiles established previously (Cabezas et al., 2012). Quantity and length of the PCR products were examined by 1% gel electrophoresis against known DNA standards. PCR reactions were sent to Macrogen Inc. (Korea, www.macrogen.com) for purification and direct sequencing in both directions. Electropherograms were assembled in Sequencher v4.9 and sequences were initially aligned in Bioedit v7.0.9 (Hall, 1999) together with 16S and COI sequences from previous works (Cabezas et al., 2009, 2011; Machordom and Macpherson, 2004; Macpherson and Machordom, 2005; Rodríguez-Flores et al., 2019). Final alignments of each of the loci were performed using MAFFT (Katoh et al., 2002). Uncorrected divergences (p) were calculated using MEGA 10.04 (Kumar et al., 2018). GenBank accession numbers for the new sequences are given in Table 1. We have not provided the divergence values among all pairs of closely related species because in the genus *Munida* the amount of molecular data is still scarce (excluding the present paper, the sequences of only 72 species are available). Nevertheless, when the molecular data from a new species and its morphological closest relative are available, we have included the divergence values in the *Remarks*.

Results

Table 1. Specimens studied for mitochondrial DNA sequences (COI and 16S), including registration codes, survey, station, and GenBank accession numbers

Species	Reg. no.	16S	COI	Survey
Munida agave	NMV J56099	MK847949	MK848000	SS05/2007 161
Munida agave	NMV J56008	MK847961	MK848011	SS05/2007 116
Munida asprosoma	NMV J56393	MK847955	MK848006	SS05/2007 155
Munida asprosoma	NMV J56016	MK847971	MK848022	SS05/2007 68
Munida asprosoma	NMV J57258	MK847950	MK848001	SS05/2007 155
Munida babai	NMV J55042	na	MK848021	SS10/2005 170
Munida distiza	NMV J56487	MK847947	MK847998	SS05/2007 11
Munida leeuwin sp. nov.	NMV J55046	MK847968	MK848018	SS10/2005 170
Munida leeuwin sp. nov.	NMV J56100	MK847954	MK848005	SS05/2007 82
Munida leeuwin sp. nov.	NMV J55046	MK847967	MK848017	SS10/2005 170
Munida gracilis	NMV J55107	MK847963	MK848013	SS10/2005 32
Munida gracilis	NMV J55107	MK847964	MK848014	SS10/2005 32
Munida gracilis	SAM C7658	MK847932	na	BPZ 2010 500
Munida compressa	NMV J55980	MK847946	na	SS05/2007 176
Munida compressa	NMV J55981	MK847944	MK847996	SS05/2007 189
Munida endeavourae	NMV J59312	MK847934	MK847986	TT01/2008 J2-390-015
Munida endeavourae	NMV J59310	MK847933	na	TT01/2008 J2-389-006
Munida gordoae	NMV J56420	MK847957	MK848008	SS05/2007 62
Munida gordoae	NMV J56420	MK847956	MK848007	SS05/2007 62
Munida abrolhos sp. nov.	NMV J55279	MK847962	MK848012	SS05/2007 70
Munida abrolhos sp. nov.	NMV J55262	MK847943	MK847995	SS05/2007 1
Munida leagora	NMV J56018	MK847951	MK848002	SS05/2007 77
Munida leagora	NMV J56004	MK847970	MK848020	SS05/2007 143
Munida leagora	NMV J56004	MK847969	MK848019	SS05/2007 143
Munida leagora	NMV J55999	MK847942	MK847994	SS05/2007 143
Munida pectinata	NMV J55268	MK847939	MK847991	SS05/2007 62
Munida philippinensis	NMV J56003	MK847953	MK848004	SS05/2007 143
Munida philippinensis	NMV J56003	MK847952	MK848003	SS05/2007 143
Munida compacta	NMV J56411	MK847941	MK847993	SS05/2007 57
Munida compacta	NMV J56402	MK847937	MK847989	SS05/2007 15
Munida compacta	NMV J56412	MK847938	MK847990	SS05/2007 56
Munida roshanei	NMV J55991	MK847958	MK848009	SS05/2007 97
Munida roshanei	NMV J56009	MK847960	na	SS05/2007 125
Munida roshanei	NMV J56400	MK847940	MK847992	SS05/2007 116
Munida julumunyju sp. nov.	NMV J55064	MK847966	MK848016	SS10/2005 152
Munida julumunyju sp. nov.	NMV J55979	MK847945	MK847997	SS05/2007 34
Munida heteracantha	NMV J55038	MK847965	MK848015	SS10/2005 146
Munida galalala sp. nov.	WAM C78558	MK847959	MK848010	SS05/2007 156
Munida jurunjurun sp. nov.	WAM C78561	MK847948	MK847999	SS05/2007 63
Munida lutruwita sp. nov.	NMV J67480	MK847935	MK847987	TT01/2008 J2-387-022
Munida lutruwita sp. nov.	NMV J67474	MK847936	MK847988	TT01/2008 J2-387-023

Systematics

Munididae Ahyong, Baba, Macpherson and Poore, 2010

Munida abrolhos sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:14DA5265-E0E5-47B5-B4B0-93296A355921

Figures 1, 2, 3A

Munida sp. MoV 5214. — Poore et al., 2008: 21 (south-western Australia, 201–206 m).

Munida aff. *rubiesi*. — Poore et al., 2008: 20 (part), unnumbered fig. — McEnnulty et al., 2011: app. 1.

Munida sp. MoV 5526. — Poore et al., 2008: 21.

Munida keiensis. — McEnnulty et al., 2011: app. 1.

Type material. Holotype: WAM C78556, ovigerous female (cl 23 mm, pcl 14 mm), Abrolhos, Western Australia, 29° 00.594' S, 113° 42.78' E to 29° 01.512' S, 113°43.32' E, 700–704 m, SS10/2005/85, 2 December 2005.

Paratypes (all Western Australia): NMV J55036, 6 ovigerous females (cl 18.9 mm, pcl 11.2 mm to cl 25.9 mm, pcl 15.7 mm), 6 females (cl 14.0 mm, pcl 8.1 mm to cl 19.0 mm, pcl 12.5 mm), 10 males (cl 15.0 mm, pcl 8.9 mm to cl 22.8 mm, pcl 14.6 mm), collected with holotype; NMV J55262, 1 ovigerous female (cl 27.5 mm, pcl 18.3 mm), 1 female (cl 14.5 mm, pcl 8.4 mm), Barrow L1 transect, 20° 59.412' S, 114° 07.896' E to 20° 59.13' S, 114° 08.394' E, 700 m, SS05/2007/1, 9 June 2007; NMV J55279, 1 specimen, Mermaid L24 transect, 16° 44.286' S, 119° 15.042' E to 16° 43.794' S, 119° 15.48' E, 693–698 m, SS05/2007/70, 17 June 2007; WAM C78557, 1 male (cl 22.6 mm, pcl 13.0 mm), Ningaloo South, 22° 03.57' S, 113° 43.74' E to 22° 04.026' S, 113° 43.26' E, 658–754 m, SS10/2005/149, 10 December 2005.

Description. Carapace. Length and width subequal, widest at midlength. Dorsal surface with main transverse ridges mostly uninterrupted, without secondary transverse striae between main ridges; ridges and striae lined with short, non-iridescent setae. Gastric region with large pair of epigastric spines behind supraocular spines and 2 or 3 pairs of small epigastric spines; without median row of spines behind rostrum. Hepatic region granular; parahepatic spine present. Anterior part of branchial region between cervical groove and postcervical groove with 1 or 2 ridges and sometimes 1or 2 short striae; postcervical spine present; posterior part of branchial region with 5 transverse ridges (excluding posterodorsal ridge). Cardiac region with 3 main transverse ridges. Intestinal region with 2 lateral striae; posterodorsal ridge distinct, without secondary stria. Frontal margin inclined posteriorly at 110° from midline. Lateral margin slightly convex; anterolateral spines parallel, directed slightly upwards, reaching sinus between rostrum and supraocular spine; hepatic marginal spine anterior to cervical groove, much shorter than anterolateral spine; branchial margin with 4, occasionally 5, spines (additional third spine small). Rostrum spiniform; curving dorsally, 0.6–0.7 × pcl; supraocular spine length 0.3 length × rostrum length. Epistomial ridge straight, ending at antennal gland; mesial protuberance distinct.

Thoracic sternum. Median length of sternal plastron (sternites 4–7) 0.6 × width of sternite 7. Thoracic sternites suface smooth, sternites 4 with few striae. Sternite 3 0.5 × width of sternite 4. Sternite 4 anterior margin subtriangular, narrowly contiguous with sternite 3.

Abdomen. Somite 2 with 8–10 large spines, evenly spaced along anterior ridge; with stria behind anterior ridge. Somites 3–4 with 2 striae behind anterior ridge. Somite 6 posteromedian margin slightly concave. Telson with numerous transverse squamae; greatest width 1.6 × midlength; anterolateral margin concave.

Eye. Maximum corneal diameter 0.35 × distance between anterolateral spines.

Antennule. Basal article (distal spines excluded) not overreaching corneae; distolateral and distomesial spines subequal; 2 lateral spines, proximal smaller, longer lateral spine reaching end of distal spines.

Antenna. Article 1 with distomesial spine reaching distal margin of article 2. Article 2 distomesial spine nearly reaching distal margin of article 4; distolateral spine reaching midlength of article 3. Articles 3 and 4 unarmed.

Maxilliped 3. Ischium 1.8 × length of merus, with small flexor distal spine. Merus flexor margin with large spine and small distal spine; extensor margin without distal spine.

P1. 2.0–2.5 pcl, with plumose setae on inner margins, and some iridescent setae, merus 0.8–0.9 pcl, with row of 6 spines on dorsal margin; distomesial spine reaching midlength of carpus. Carpus 0.4 × length of merus, length 0.9–1.1 × width, with 5 spines along the mesial margin. Propodus 1.0–1.4 × merus length, fingers longer than palm, 0.5–0.6 × total propodus length; pollex with subdistal spine, outer margin unarmed; dactylus outer margin unarmed.

P2–4. Long, slender, with few small scales on lateral surfaces of meri, carpi and propodi; extensor margin with plumose setae and few iridescent setae. P2 and P3 similar in length, P4 shorter (P3 merus 0.9–1.0 × length of P2 merus, P4 merus 0.8 × length of P3 merus). P2 1.9–2.1 × pcl; merus 0.6–0.8 × pcl, length 6 × width, 3–4 × carpus length and 1.6 × propodus length, extensor margin with 9 spines including distal spine, flexor margin with 4 spines and well-developed distal spine; carpus with 2 extensor spines a distal flexor spine; propodus length 5.5–6.5 × height, with 5 movable flexor spines; dactylus 0.8–0.9 × propodus length, gently curved, length 6–7 × width, extensor margin densely lined with stiff short setae on distal half, flexor margin with 8 small moveable spines, space between spines increasing distally, unarmed along distal 1/5. End of P2 carpus overreaching end of P1 merus. P3 with similar spination and article proportions as P2; merus, propodus and dactylus as long as those of P2. P4 length 0.85 × P2 length; merus 0.5–0.6 × pcl; merocarpal articulation reaching hepatic marginal spine of carapace.

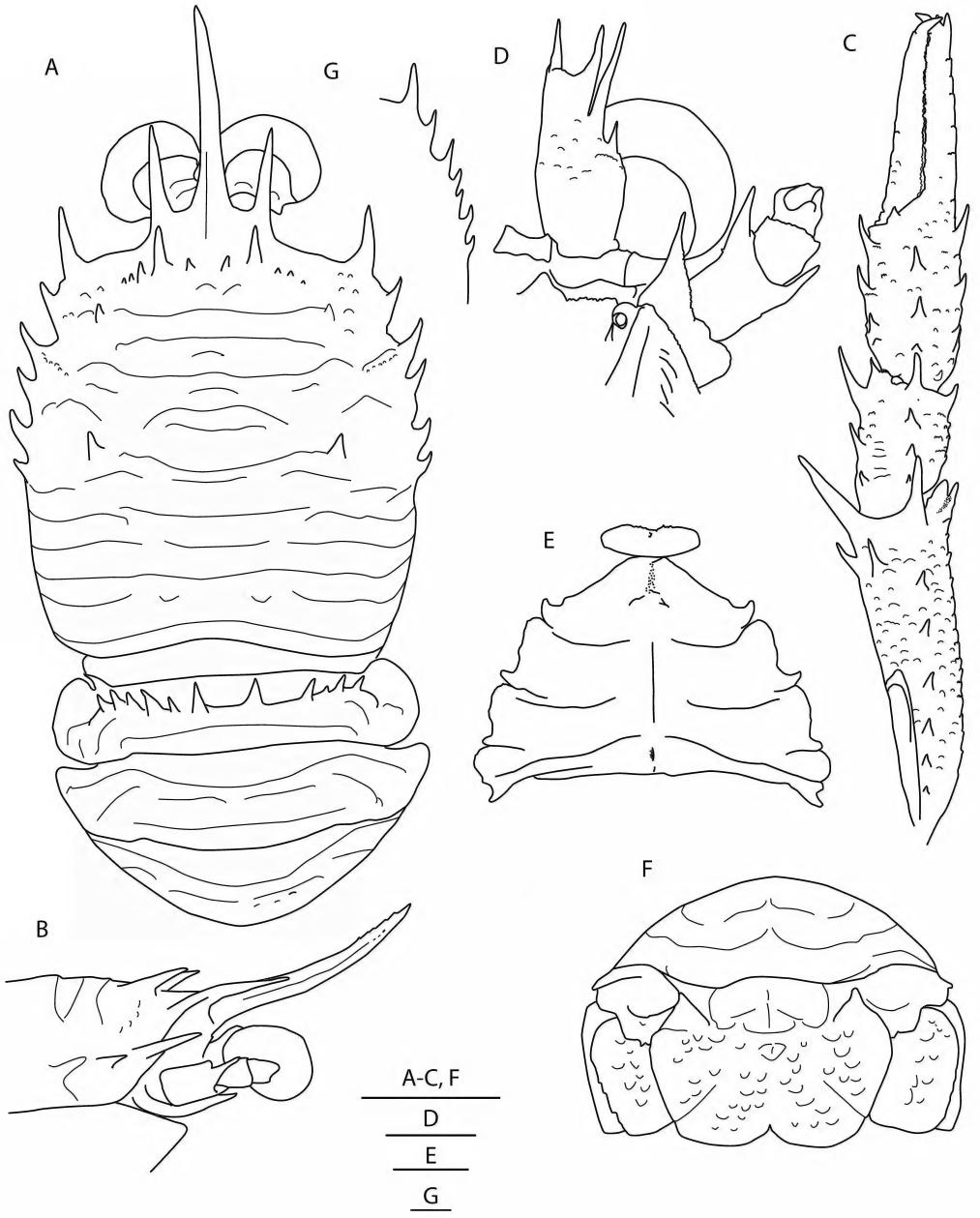
Egg diameter. 0.5 mm.

Colour. Carapace and abdominal somites 2–3 pink. Rostrum and supraocular spines white. P1 pale pink with white fingers, P2–4 pale pink on meri and carpi, white on propodi and dactyli.

Genetic data. COI and 16S; see Table 1.

Etymology. After the type locality near the Abrolhos Islands; used as a noun in apposition.

Remarks. *Munida abrolhos* sp. nov. is similar to *M. andamanica* Alcock, 1894, *M. rosula* Macpherson, 1994, and *M. curvirostris* Henderson, 1885, with a dorsally curving spiniform rostrum, P1



Figue 1. *Munida abrolhos* sp. nov., holotype, ovigerous female cl 23 mm, pcl 14 mm (WAM C78556): A, carapace and abdomen, dorsal view; B, rostrum, lateral view; C, right chela, dorsal view; D, left antenna and antennule, ventral view; E, sternum; F, abdominal somite 6, telson and right uropod. G, ovigerous female cl 22.9 mm, pcl 14.4 mm (NMV J55036), anterolateral margin of carapace. Scale: A–C, F = 5 mm, D, E, G = 2 mm.

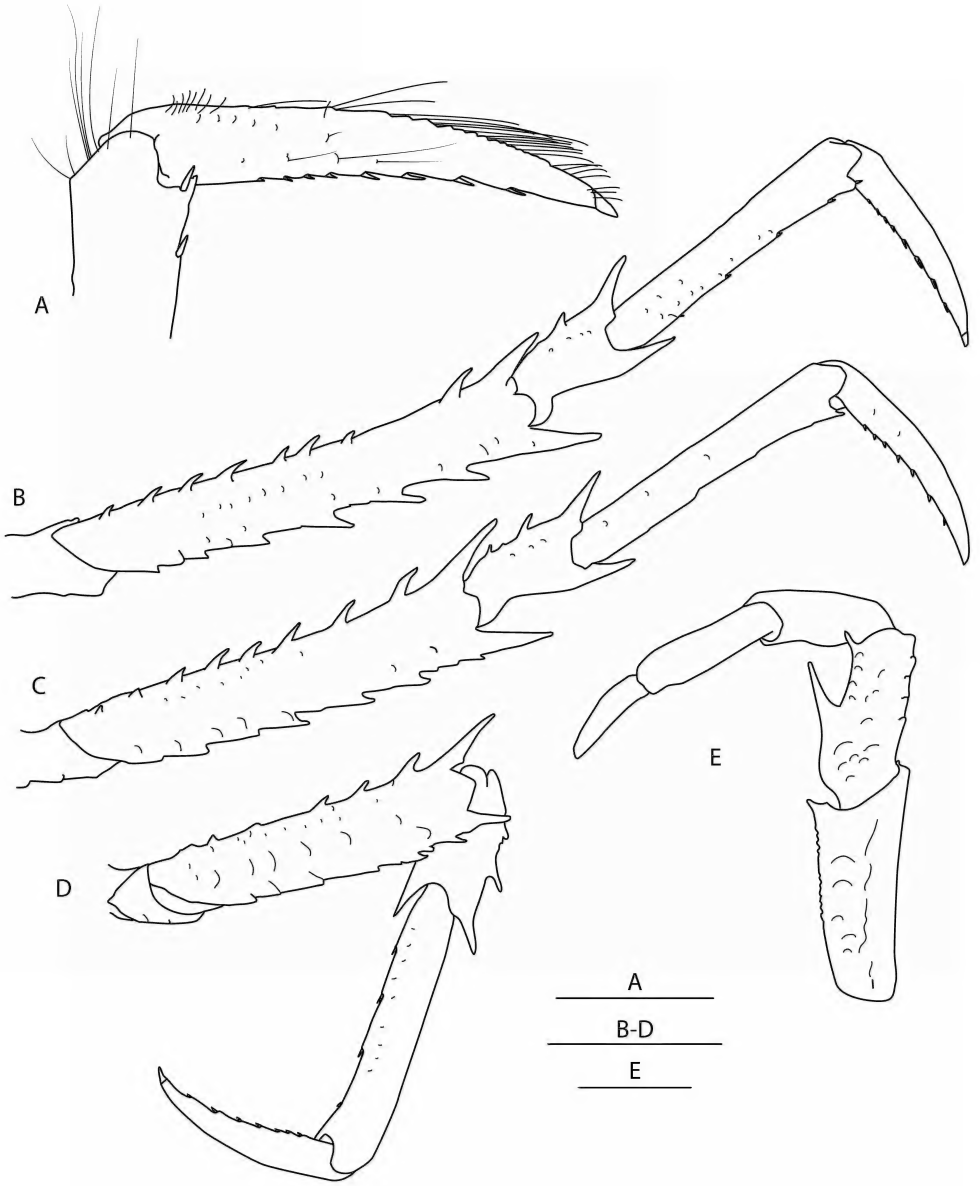


Figure 2. *Munida abrolhos* sp. nov., holotype, ovigerous female cl 23 mm, pcl 14 mm (WAM C78556): A, right P2 dactylus, lateral view; B, right P2, lateral view; C, right P3, lateral view; D, right P4 lateral view; E, left maxilliped 3, lateral view. Scale A, E = 2 mm, B–D = 5 mm

Figure 3. A, *Munida abrolhos* sp. nov., female paratype, cl 27.5 mm, pcl 18.3 mm (NMV J55262); B–D, *Munida julumunyju* sp. nov., undetermined paratype from NMV J55979, juvenile paratype, cl 9.2 mm, pcl 10.8 mm (NMV J55061), juvenile paratype cl 10.9 mm, pcl 6.6 mm (NMV J55062); E, *Munida lutruwita* sp. nov. ovigerous female, cl 14.3 mm, pcl 10.6 mm, (AM P103229). Photos: K. Gowlett-Holmes, CSIRO.

fixed finger with only subterminal spine (without marginal spines on lateral margin), and abdominal somite 2 with a row of 6–8 spines and at most 4 transverse ridges. Most clearly the new species differs from these species as it usually has only 4 branchial spines, although sometimes a smaller third branchial spine is present. In addition, postcervical spines, present in *M. abrolhos* sp. nov., are always absent in the aforementioned species.

Of those species with 4 branchial spines, *M. abrolhos* sp. nov. is most similar to *M. keiensis* Baba, 2005, in having subequal distal spines of the basal antennular article, and the distomesial spine of antennal article 2 overreaching article 3 but not distinctly overreaching article 4. The two species can be distinguished by the shape of the anterior margin of thoracic sternite 4, which is broadly rounded in *M. keiensis* but subtriangular in *M.* sp. nov.

Sequence divergence between *M. abrolhos* sp. nov. and *M. rosula* is 3% for COI and 0.8% for 16S.

Distribution. Presently known only from off Western Australia, 658–754 m.

Munida galalala sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:83168BC4-60EA-4710-A32B-42AAFFF985CA

Figures 4, 5

Type material. Holotype. WAM C78558, male (cl 17.8 mm, pcl 11.5 mm), Western Australia, Leveque L27 transect, 14° 33.432' S, 121° 20.388' E to 14° 2.772' S, 121° 19.644' E, 924–1101 m, SS05/2007/156, 3 July 2007 to 4 July 2007.

Description. Carapace. Length 1.1 × greatest width, widest at midlength. Dorsal surface with main transverse ridges mostly uninterrupted and some short secondary transverse striae between main ridges on anterior half; ridges and striae lined with short, non-iridescent setae. Gastric region slighly elevated, with 2 pairs of epigastric spines, longest pair behind supraocular spines. Hepatic region granular; parahepatic spine absent. Anterior part of branchial region between cervical groove and postcervical groove with few short scale-like ridges and tubercles; postcervical spine absent; posterior part of branchial region with 5 main transverse ridges (excluding posterodorsal ridge) and few short secondary striae laterally between main ridges. Cardiac region with 4 main transverse ridges. Intestinal region with short median stria; posterodorsal ridge distinct, slightly convex medially, without secondary stria. Frontal margin inclined posteriorly at 110° from midline. Lateral margins slightly convex; anterolateral spines parallel, horizontal, reaching sinus between rostrum and supraocular spine; marginal hepatic spine anterior to cervical groove also strong, although distinctly shorter than anterolateral spine; branchial margin with 5 spines. Rostrum spiniform, gentle curving upwards, length 0.7 pcl; supraocular spine 0.45 × length of rostrum. Epistomial ridge curved ending anterior to antennal gland; mesial protuberance distinct.

Thoracic sternum. Surface smooth, without striae. Sternite 3 0.4 width of sternite 4; median length of sternal plastron (sternites 4–7) 0.6 width of sternite 7. Sternite 4 anterior margin subtrapezoid, broadly contiguous with sternite 3.

Abdomen. Somite 2 with 7 prominent spines along anterior transverse ridge. Somites 2–4 each with 1 uninterrupted stria behind anterior ridge, without striae at lateral margins. Somite 6 posteromedian margin almost straight. Telson with numerous transverse squamae; greatest width 1.5 × median length; anterolateral margin concave.

Eye. Maximum corneal diameter 0.15 × distance between anterolateral spines.

Antennule. Basal article (distal spines excluded) overreaching corneae; well-developed distolateral spine much longer than short distomesial spine; 2 lateral spines, proximal smaller, not exceeding distal spines.

Antenna. Article 1 with strong distomesial spine not reaching distal margin of article 2. Article 2 distomesial spine not overreaching distal margin of article 3; distolateral spine reaching distal margin of article 3. Article 3 distomesial spine almost reaching distal margin of article 4. Article 4 unarmed.

Maxilliped 3. Ischium 1.3 × merus length, with small flexor distal spine. Merus with 2 large spines on flexor margin and 1 small spine; extensor margin unarmed.

P1. 3.0 × pcl, covered in plumose setae, without iridescent setae, merus 1.2 × pcl, with row of 6 dorsal spines and 2 rows of spines on mesial margin; distal spines strong, distomesial spine not reaching midlength of carpus. Carpus 0.6 × merus length, length 2.6 × width, with spines along mesial and dorsal margins. Propodus 1.2 × merus length, fingers slightly shorter than palm, 0.5 × total propodus length; pollex with small subdistal spine, margin unarmed; dactylusouter margin unarmed.

P2–4. Moderately long, slender, with numerous scales on lateral surfaces of meri; extensor margin with row of plumose setae. P2 length 2.1 × pcl; merus as long as pcl, length 7× height, 3.5 × carpus length and 1.4 × propodus length, with well-developed spines on extensor margin, increasing in size distally, flexor margin with row of small spines and well-developed distal spine; carpus with large spine and distal spine on extensor margin, distal spine on flexor margin; propodus length 6.5 × height, with 5 small movable flexor spines; dactylus compressed, slightly curved, 0.6 × propodus length, length 5.5 × width, with 9 movable spines evenly spaced along flexor margin including spine at base of unguis. End of P2 carpus reaching end of P1 merus. P3 missing. P4 length 0.8 × P2 length; merus 0.7 × pcl; merocarpal articulation almost reaching hepatic marginal spine of carapace.

Genetic data. COI and 16S; see Table 1.

Etymology. Named *galalala*, meaning lobster in Dambimangari language, used as a noun in apposition.

Remarks. *Munida galalala* sp. nov. belongs to the group of species having five spines on the lateral branchial margins of the carapace, smooth thoracic sternites, small eyes, and spines on the anterior ridge of abdominal somite 2. The antennal peduncle is most similar to *Munida parvioculata* Baba, 1982, both species having a distinct distomesial spine on antennal peduncle article 3. The new species differs in:

- the generally smooth surface of the carapace with widely spaced transverse striae, compared to rugose with interrupted transverse ridges in *M. parvioculata*

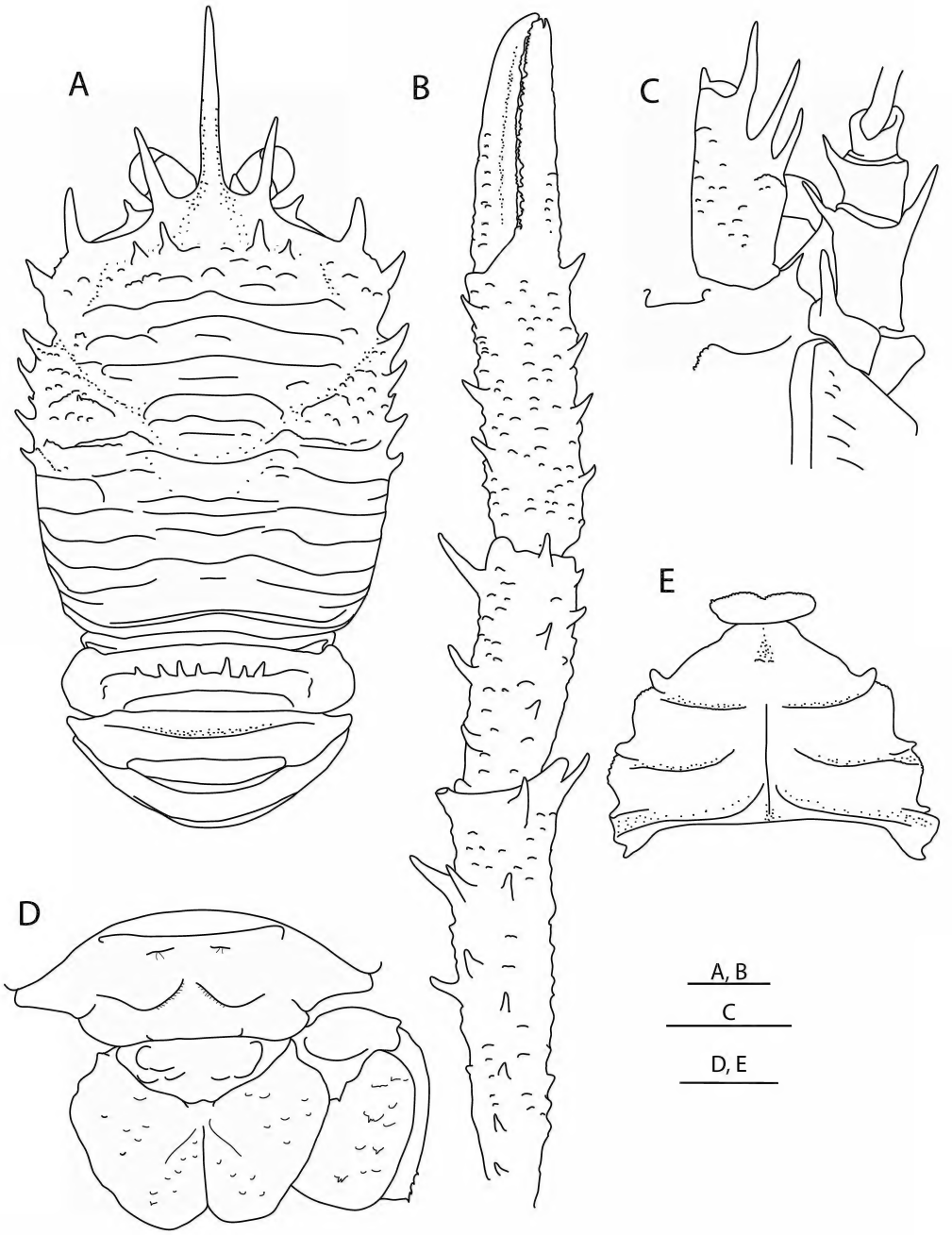


Figure 4. *Munida galalala* sp. nov., holotype, male 17.8 mm (WAM C78558): A, carapace and abdomen, dorsal view; B, right chela, dorsal view; C, left antenna and antennule, ventral view; D, abdominal somite 6, telson and right uropod. E, sternum. Scale: A–E = 2 mm.

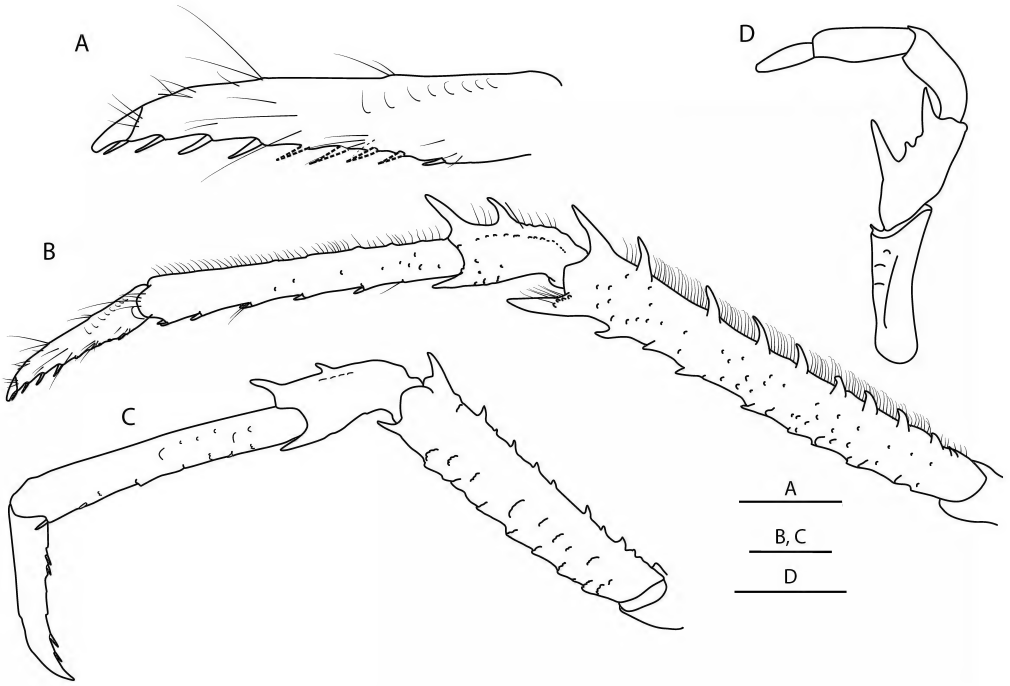


Figure 5. *Munida galalala* sp. nov., holotype, male 17.8 mm (WAM C78558): A, left P2 dactylus, lateral view; B, left P2, lateral view; C, left P4, lateral view; D left maxilliped 3, lateral view. Scale A = 1 mm, B–D = 2 mm

- the unarmed lateral margin of the cheliped pollex (with 2 spines in *M. parvioculata*)

- a row of 7 spines on abdominal somite 2 versus a single pair in *M. parvioculata*.

Munida galalala can be distinguished from all other species in this group (i.e. *M. clevai* Macpherson, 2009, *M. ampliantennulata* Komai, 2011, *M. profunda* Macpherson and de Saint Laurent, 1991, *M. endeavourae* Ahyong and Poore, 2004, *M. pollioculus* Komai and Higashiji, 2016, and *M. typhle* Macpherson, 1994) by the presence of a spine on antennal peduncle article 3.

Distribution. Presently known only from off north-western Australia, 924–1101 m.

Munida julumunyju sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:A4CFAE49-1832-4C56-BDED-A68F843BB9F4

Figures 3B–D, 6, 7

Munida rubridigitalis. — Poore et al., 2008: 20, unnumbered fig. (upper right) — McEnnulty et al., 2011: app. 1, 2.

Type material. Holotype: WAM C78559, female cl 22.4 mm, pcl 15.8 mm), Western Australia, Onslow L19 transect, 20° 07.962' S, 114° 58.71' E to 20° 07.584' S, 114° 58.416' E, 415–470 m, SS05/2007/15, 11 June 2007.

Paratypes (all Western Australia): NMV J56082, 1 female (cl 24.4 mm, pcl 16.3 mm), collected with holotype; NMV J55979, 1 male (cl 22.0 mm, pcl 15.0 mm), 1 ovigerous female (cl 18.8 mm, pcl 13.3 mm), Dampier L20 transect, 19° 43.776' S, 115° 21.216' E to 19° 43.56' S, 115° 20.598' E, 389–423 m, SS05/2007/34, 12 June 2007; NMV J55061, 1 juvenile (cl 9.2 mm, pcl 10.8 mm), Carnarvon, 24° 33.12' S, 112° 15.12' E to 24° 33.804' S, 112° 15.18' E, 396–404 m, SS10/2005/122, 7 December 2005; NMV J55062, 1 juvenile (cl 10.9 mm, pcl 6.6 mm), Red Bluff, 23° 59.196' S, 112° 32.04' E to 23° 59.724' S, 112° 31.74' E, 411 m, SS10/2005/130, 8 December 2005; WAM C78560, 2 males (cl 22.6 mm, pcl 14.8 mm; cl 27.0 mm, pcl 19.2 mm), 1 female (cl 22.6 mm, pcl 16.0 mm), Point Cloates, 22° 50.808' S, 113° 20.28' E to 22° 51.228' S, 113° 19.98' E, 420–430 m, SS10/2005/137, 9 December 2005; NMV J55060, 1 male (cl 24.2 mm, pcl 16.7 mm), Ningaloo South, 22° 04.374' S, 113° 45.36' E to 22° 04.968' S, 113° 45.36' E, 391–396 m, SS10/2005/148, 10 December 2005; NMV J55064, 1 male (broken rostrum; pcl 10.8 mm), Ningaloo South, 22° 04.314' S, 113° 45.36' E to 22° 04.854' S, 113° 45.36' E, 387–399 m, SS10/2005/151, 10 December 2005; NMV J55059, 1 female (cl 23.2 mm, pcl 15.9 mm), Ningaloo North, 21° 58.212' S, 113° 47.46' E to 21° 58.806' S, 113° 47.1' E, 373–382 m, SS10/2005/165, 12 December 2005; NMV J55058, 2 males (cl 17.0 mm, pcl 11.1 mm; cl 25.8 mm, pcl 18.4 mm), Barrow Island, 21° 00.402' S, 114° 22.86' E to 21° 00.042' S, 114° 22.5' E, 399–408 m, SS10/2005/172, 13 December 2005.

Other material examined. New Caledonia: MNHN-IU-2014-15475, 2 females (cl 14.6 mm, pcl 9.1 mm; cl 18.5, pcl 11.5), 3 males (cl 14.3–16.0 mm, pcl 8.5–10.1 mm), east coast, 21° 14.84' S 165° 55.49' E, 450–

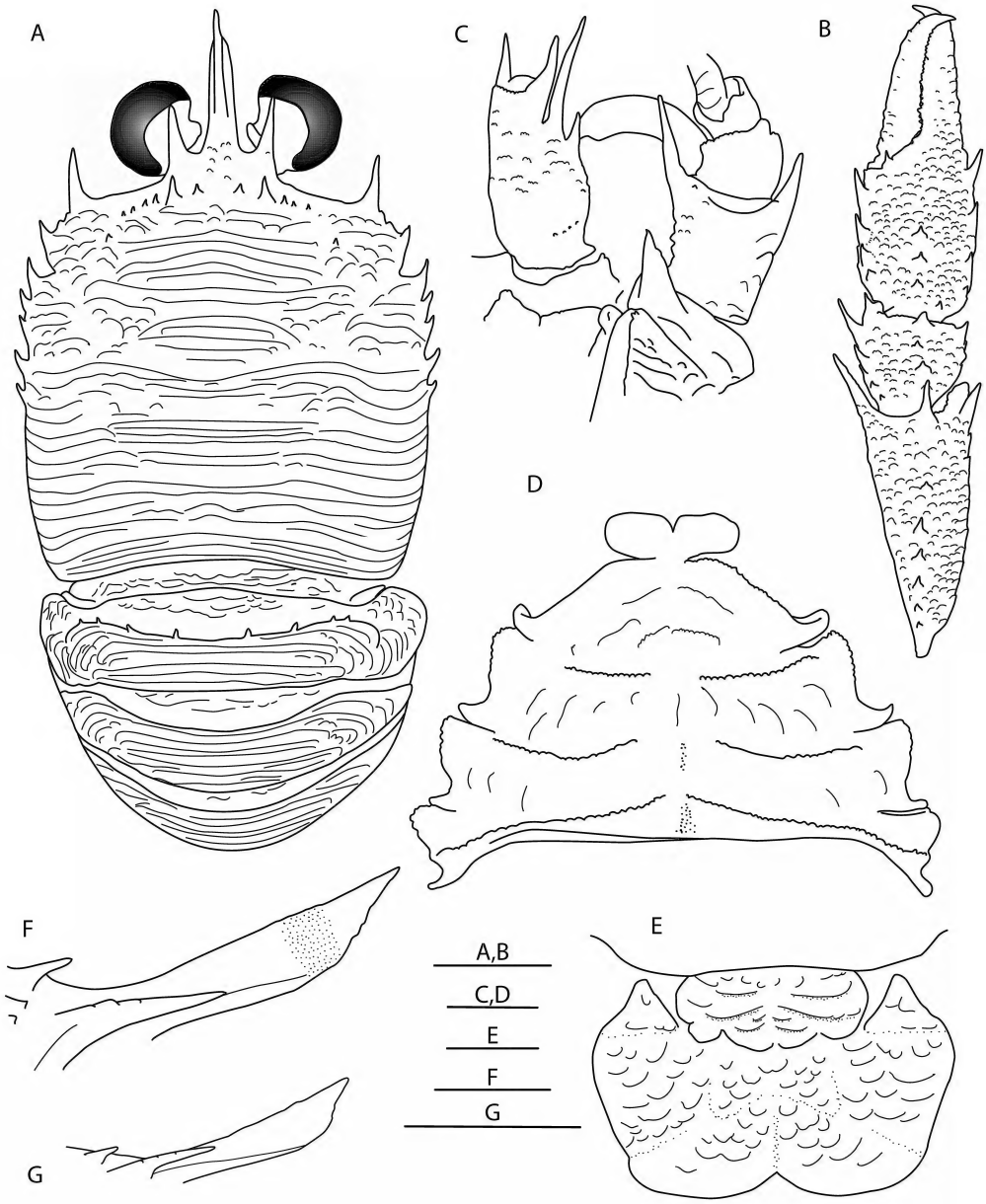


Figure 6. *Munida julumunyju* sp. nov., holotype, ovigerous female cl 22.4 mm, pcl 15.8 mm (WAM C78559): A, carapace and abdomen, dorsal view; B, right chela, dorsal view; C, right antenna and antennule, ventral view; D, sternum; E, telson; F, rostrum, lateral view. *Munida julumunyju*, New Caledonia, male cl. 18.2, pcl 12.2 (MNHN-IU-2014-15475): G, rostrum, lateral view. A–D, G = 5 mm, E–F = 2 mm.

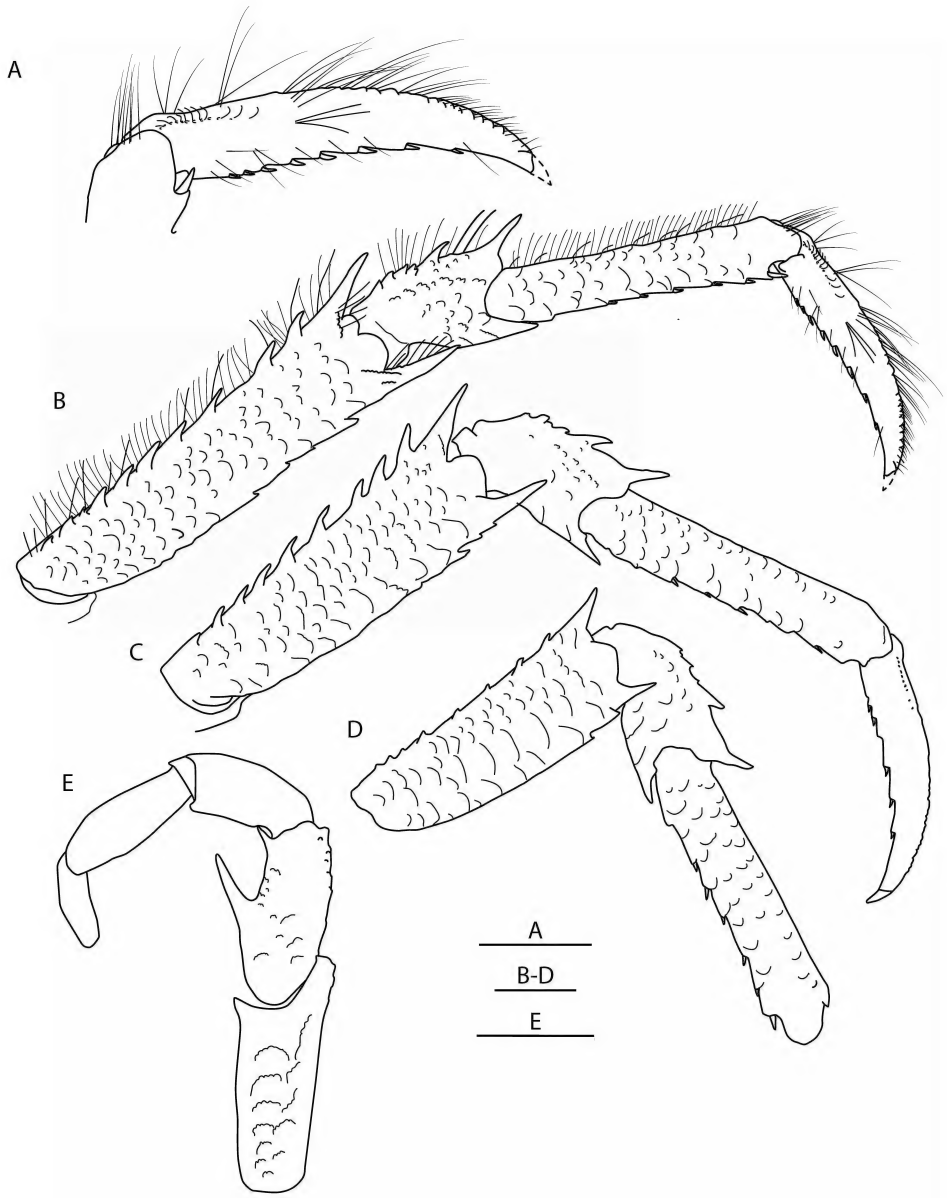


Figure 7. *Munida julumunyju* sp. nov., holotype, ovigerous female cl 22.4 mm, pcl 15.8 mm (WAM C78559). A, right P2 dactylus, lateral view; B, right P2, lateral view; C, right P3, lateral view; D, right P4, lateral view; E, left maxilliped 3, lateral view. Scale A–E = 2 mm.

490 m, HALIPRO 1 CP869, 23, March 1994; MNHN-IU-2014-15474, 1 female (cl 15.8 mm, pcl 10.3 mm), Norfolk Ridge, 22° 10' S 167° 15.2' E, 495–515 m, BIOCAL CP109, 9 September 1985.

Description. Carapace. Length 0.9 × greatest width, widest at midlength. Dorsal surface with main transverse ridges mostly uninterrupted, with secondary transverse striae between main ridges; ridges and striae lined with short, non-iridescent setae. Gastric region with 3–6 pairs of epigastric spines, longest pair behind supraocular spines. Hepatic region with short striae; small parahepatic spine sometimes present. Anterior part of branchial region between cervical groove and postcervical groove with about 6 ridges and some shorter striae; posterior part of branchial region with about 12 transverse ridges (excluding posterodorsal ridge). Cardiac region with 3 or 4 main transverse ridges. Intestinal region with 2 or 3 striae; posterodorsal ridge distinct, with secondary stria. Frontal margin inclined posteriorly at 105° from midline. Lateral margin slightly convex; anterolateral spines parallel, horizontal, just reaching sinus between rostrum and supraocular spine; marginal hepatic spine anterior to cervical groove, much shorter than anterolateral spine; branchial margins with 5 spines. Rostrum laterally compressed; dorsal margin straight, inclined dorsally, ventral margin strongly convex, deepest slightly anterior to midlength, length 0.4–0.5 × pcl; supraocular spine 0.4 × length of rostrum. Epistomial ridge straight, ending at antennal gland; mesial protuberance distinct.

Thoracic sternum. Median length of sternal plastron (sternites 4–7) 0.5 × width of sternite 7. Sternites 4–5 with striae; sternite 6 with few striae. Sternite 3 0.4 width of sternite 4. Sternite 4 anterior margin subtrapezoid, narrowly contiguous with sternite 3.

Abdomen. Somite 2 with 8 small spines evenly spaced along anterior ridge. Somites 2–4 with about 5, 7 and 12 uninterrupted striae behind anterior ridge, respectively, and squamae at lateral margins. Somite 6 posteromedian margin almost straight. Telson with numerous transverse squamae; greatest width 1.7 × median length; anterolateral margin concave.

Eye. Maximum corneal diameter 0.3 × distance between anterolateral spines.

Antennule. Basal article (distal spines excluded) not overreaching corneae; distolateral and distomesial spines subequal; 2 lateral spines, proximal smaller, longer lateral spine exceeding distal spines.

Antenna. Article 1 with distomesial spine reaching midlength of article 2. Article 2 with distomesial spine reaching distal margin of article 4; distolateral spine almost reaching distal margin of article 3. Article 3 and 4 unarmed.

Maxilliped 3. Ischium 1.8 × merus length, with flexor distal spine. Merus with large spine and small distal spine on flexor margin; extensor margin unarmed.

P1. 1.6–1.9 pcl (females), 1.7–2.1 pcl (males), covered in plumose setae and iridescent setae in inner margin; merus 0.6–0.7 pcl (females), 0.7–0.8 pcl (males), with row of 5 small spines on dorsal margin; distomesial spine reaching midlength of carpus. Carpus 0.4 (females), 0.4–0.5 (males) × merus length, length 0.9–1.1 × width, with 5 spines along the mesial margin. Propodus 1.2–1.3 (females), 1.1–1.6 (males) × merus length, dactylus longer than palm, 0.5 × total propodus length; dactylus and pollex outer margin unarmed.

P2–4. Relatively stout, with scales on lateral surface of meri, carpi and propodi; extensor margin with plumose setae and iridescent setae. Meri shorter posteriorly (P3 merus 0.9 × P2 merus length, P4 merus 0.8 × P3 merus length). P2 1.8–2.2 × pcl; merus 0.6–0.8 × pcl, length 4 × width, 2.6–3.0 × carpus length and 1.3–1.6 × propodus length, extensor margin with 11–17 spines, flexor margin with acute ridges and well-developed distal spine; carpus with 2 large spines and 2 or 3 smaller spines on extensor margin, distal spine on flexor margin; propodus length 5 × height, with 6–8 movable flexor spines; dactylus 0.7–0.9 × propodus length, curved, length 5–6 × width, extensor margin densely lined with stiff long setae on distal half, flexor margin with 8–12 spines, space between spines increasing distally, unarmed along distal 1/5. End of P2 carpus almost reaching end of P1 merus. P3 with similar spination and article proportions as P2; merus slightly shorter than P2 merus (0.9); propodus and dactylus as long as those of P2. P4 length 0.8 × P2 length; merus 0.5 × pcl; merocarpal articulation reaching hepatic marginal spine of carapace.

Egg diameter. 0.5 mm.

Colour. Carapace and abdominal somites 2–3 orange, remaining abdomen and telson white. Rostrum white with red subdistal spot, supraocular spines orange. Chelipeds and walking legs with transverse white/pale orange and dark orange bands; distal half of palm and proximal half of cheliped fingers orange, distal half of fingers of cheliped white; dactyli of walking legs white.

Genetic data. COI and 16S; see Table 1.

Etymology. Named *julumunyju* with approval of the Kariyarra people. The word julumunyju means prawn in Kariyarra language; used as a noun in apposition.

Remarks. *Munida julumunyju* sp. nov. is very similar to *M. rubridigitalis* Baba, 1994, described from Queensland, Australia. Both species have a laterally compressed rostrum with a red mark and red cheliped fingers, the second abdominal somite with 8 or 9 spines along the anterior ridge and subequal distal spines on the basal antennular article. Comparison of *M. julumunyju* with paratypes of *M. rubridigitalis* and additional specimens from eastern Australia found that the two species differ chiefly in the shape of the rostrum. The rostrum of both species is laterally compressed, but shallower and more evenly tapered in *M. rubridigitalis*. In *M. rubridigitalis,* the ventral rostral margin is gently convex with the dorsal and ventral margins parallel for the proximal half or slightly more, after which they gently converge to the apex. In *M. julumunyju* sp. nov., however, the rostrum is deeper, with the dorsal and ventral margins distally diverging, reaching the greatest depth slightly anterior to the midlength and then converging to the apex, making the ventral margin more strongly convex than in *M. rubridigitalis*. In addition, *M. rubridigitalis* usually has a spine on the mesial margin of the antennal article 2 (occasionally present only on one side), which is always absent in *M. julumunyju*. Colour-in-life may also be helpful in distinguishing these species. The new species has a red patch on the pterygostomian flap below the linea anomurica, which is noted as absent in *M. rubridigitalis* by Baba (1994). In *M. julumunyju* sp. nov. the fingers are completely red with a

white tip, whereas *M. rubridigitalis* is described with only the distal half of the fingers red.

We examined six specimens identified as *M. rubridigitalis* from New Caledonia in the collections of the MNHN, and herein we identify these specimens as *M. julumunyju* sp. nov. These specimens agree with *M. julumunyju* sp. nov. in rostral form and lack of a spine on the mesial margin of antennal article 2. Specimens reported and figured from New Caledonia and the Loyalty Islands as *Munida* sp. by Macpherson (1994: fig. 13b, 90) also agree with *M. julumunyju* in rostral form and the colour of the fingers, which are described as red with a white tip. Sequence divergence between *M. julumunyju* sp. nov. and a New Caledonian specimen of *"M. rubridigitalis"* (MNHN-IU-2014-15474) is 4% (COI) and 0.6% (16S). Thus, further study is required to determine if other reported specimens of *"M. rubridigitalis"* from the New Caledonian region are conspecific with, or distinct from, *M. julumunyju* sp. nov. The apparently disjunct distribution of *M. julumunyju* sp. nov. suggests that it can be expected to occur at intermediate localities, possibly off southern Indonesia and Papua New Guinea.

Distribution. Presently known from off Western Australia, 373–450 m. New Caledonia, 450–515 m. Loyalty Islands, 540 m.

Munida jurunjurun sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:CD77DA72-B760-4983-9252-6BC62CC7CE50

Figures 8, 9

Type material. Holotype: WAM C78561, ovigerous female (cl 14.7 mm, pcl 9 mm), Western Australia, off Imperieuse Reef, 17° 35.982' S, 118° 59.076' E to 17° 38.574' S, 119° 01.26' E, 222–319 m, SS05/2007/63, 16 June 2007.

Description. Carapace. Length 1.1 × greatest width, widest at midlength. Dorsal surface with numerous uninterrupted transverse ridges and secondary transverse striae between main ridges; ridges and striae lined with short, non-iridescent setae. Gastric region with 5 pairs of epigastric spines, longest pair behind supraocular spines. Parahepatic, postcervical and dorsal branchial spine present. Anterior part of branchial region between cervical groove and postcervical groove with 3 main ridges; posterior part of branchial region with 6 main transverse ridges (excluding posterodorsal ridge) and 5 secondary striae laterally between main ridges. Cardiac region with 5 main transverse ridges. Intestinal region with transverse ridge, posterodorsal ridge and secondary stria. Frontal margin inclined posteriorly at 112° from midline. Lateral margins slightly convex; anterolateral spines parallel, horizontal, overreaching sinus between rostrum and supraocular spine; small hepatic marginal spine in front of cervical groove (0.15 × length of anterolateral spine); branchial margin with 4 spines. Rostrum spiniform, horizontal, 0.7 × pcl; supraocular spine 0.5 × length of rostrum. Epistomial ridge straight ending slightly anterior to antennal gland; mesial protuberance distinct.

Thoracic sternum. Sternal surface smooth, sternite 4 with few short striae. Sternite 3 0.4 width of sternite 4; midlength of sternal plastron (sternites 4–7) 0.5 width of sternite 7. Sternite 4 anterior margin broadly rounded.

Abdomen. Somite 2 with 2 pairs of small spines at lateral margins of anterior transverse ridge. Somites 2–4 each with 2 or 3 uninterrupted striae behind anterior ridge and some shorter striae. Somite 6 posteromedian margin almost straight. Telson with numerous transverse squamae; greatest width 2.0 × median length; anterolateral margin almost straight or shallowly concave.

Eye. Maximum corneal diameter 0.36 × distance between anterolateral spines.

Antennule. Basal article (distal spines excluded) overreaching or reaching end of corneae; 2 well-developed distal spines, distomesial slightly longer than distolateral; 2 lateral spines, proximal small, distolateral spine exceeding both distal spines.

Antenna. Article 1 with strong distomesial spine overreaching distal margin of article 4. Article 2 with strong distomesial spine overreaching distal margin of article 4; distolateral spine reaching distal margin of article 4; 2 small lateral spines on mesial margin. Articles 3 and 4 unarmed.

Maxilliped 3. Ischium 1.45 × merus length, with strong flexor distal spine; merus with strong spine on flexor margin and small spine distally, with small spine on distal extensor margin.

P1. length 3.0 × pcl, with iridescent setae on inner margin. Merus 1.25 × pcl, with a row of 5 dorsal spines and row of 5 long, close set spines on mesial margin; distal spines strong, distomesial spine not reaching midlength of carpus. Carpus 0.4 × merus length, length 2.6 × width, with spines along mesial and dorsal margins. Propodus 1.1 × merus length, fingers 0.5 × total propodus length, with 2 small distolateral spines; dactylus with small proximal spine small subdistal spine.

P2–4. Long and slender, with numerous scales on lateral surfaces of meri; margins with row of plumose setae and iridescent setae on ischium and merus. P2 length 2.6 × pcl; merus as long as pcl, length 6 × height, 4.0 × carpus length and 1.2 × propodus length, extensor margin spinose, flexor margin with small spine near distal one-fifth and well-developed distal spine; carpus extensor margin with 3 small spines (broken on right P2 of the holotype) and prominent distal spine, flexor margin with distal spine; propodus length 9.3 × height, with 11 small movable flexor spines; dactylus compressed, slightly curved, length 0.5 × propodus length and 5 × height, with 10 evenly spaced spines along distal 0.8 of flexor margin. End of P2 carpus reaching end of P1 merus. P3 with similar spination and article proportions as P2; merus slightly shorter than P2 merus (0.85); propodus and dactylus as long as those of P2. P4 length 0.9 × P2 length; merus 0.7 × pcl, 0.8 × P3 merus length; propodus 0.85 and dactylus 0.95 × length of those of P3; merocarpal articulation slightly overreaching anterolateral corner of carapace.

Genetic data. COI and 16S; see Table 1.

Etymology. Named *jurunjurun* with the approval of Bardi elders, after Jurun jurun, meaning crayfish in Bardi; used as a noun in apposition.

Remarks. *Munida jurunjurun* sp. nov. is closest to *M. acantha* Macpherson, 1994, from New Caledonia, both species having antennal articles 1 and 2 with long mesial spines overreaching article 4, antennule with distomesial spine longer than

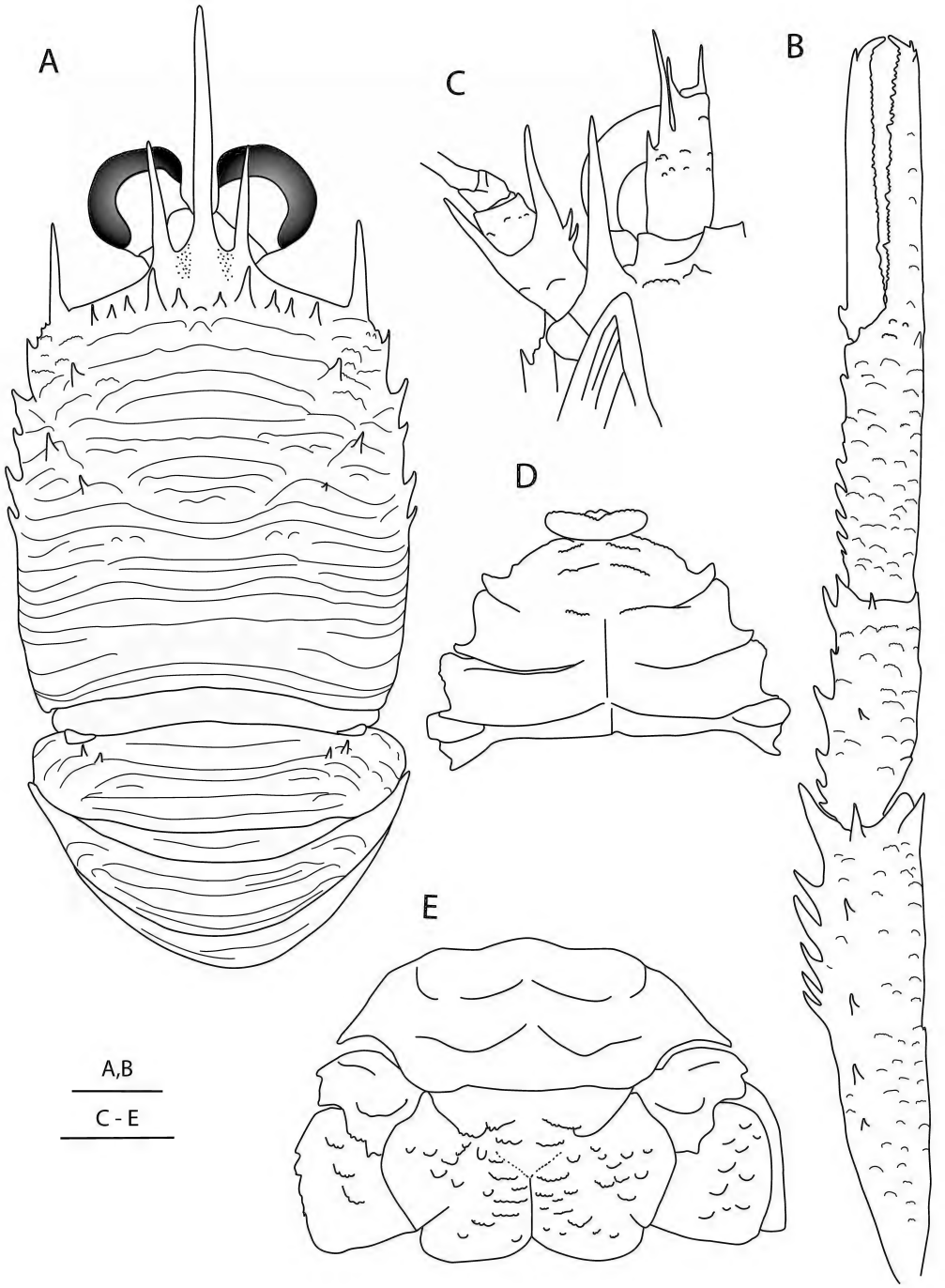


Figure 8. *Munida jurunjurun* sp. nov., holotype, ovigerous female cl 14.7 mm, pcl 9 mm (WAM C78561). A, carapace and abdomen, dorsal view; B, right chela, dorsal view; C, right antenna and antennule, ventral view; D, sternum; E, abdominal somite 6, telson and right uropod. Scale: A–E = 2 mm.

distolateral spine, a smooth thoracic sternum, and abdominal somite 2 with small spines limited to the lateral margins of the anterior ridge. The new species differs from *M. acantha* in having 4 rather than 5 branchial carapace spines. In addition, the new species has a distinct row of spines on the mesial margin of the P1 merus, which are close-set on the distal half of the article, rather than more evenly spaced along the distal 0.6 as in *M. acantha*. Sequence divergence between *M. acantha* and *M. jurunjurun* sp. nov. is 8% for COI and 3.5% for 16S.

Of those species with 4 branchial spines, *M. jurunjurun* sp. nov. is similar to *M. albiapicula* Baba and Yu, 1987, *M. zebra* Macpherson, 1994, *M. volantis* Macpherson, 2004, and *M. nesiotes* Macpherson, 1999, all of which have a long mesial spine on antennal articles 1 and 2. In these species, however, the spines on the anterior ridge of abdominal somite 2 are evenly spread along the entire margin, rather than placed at the lateral extremities.

Distribution. North-western Australia, off Imperieuse Reef, 222–319 m

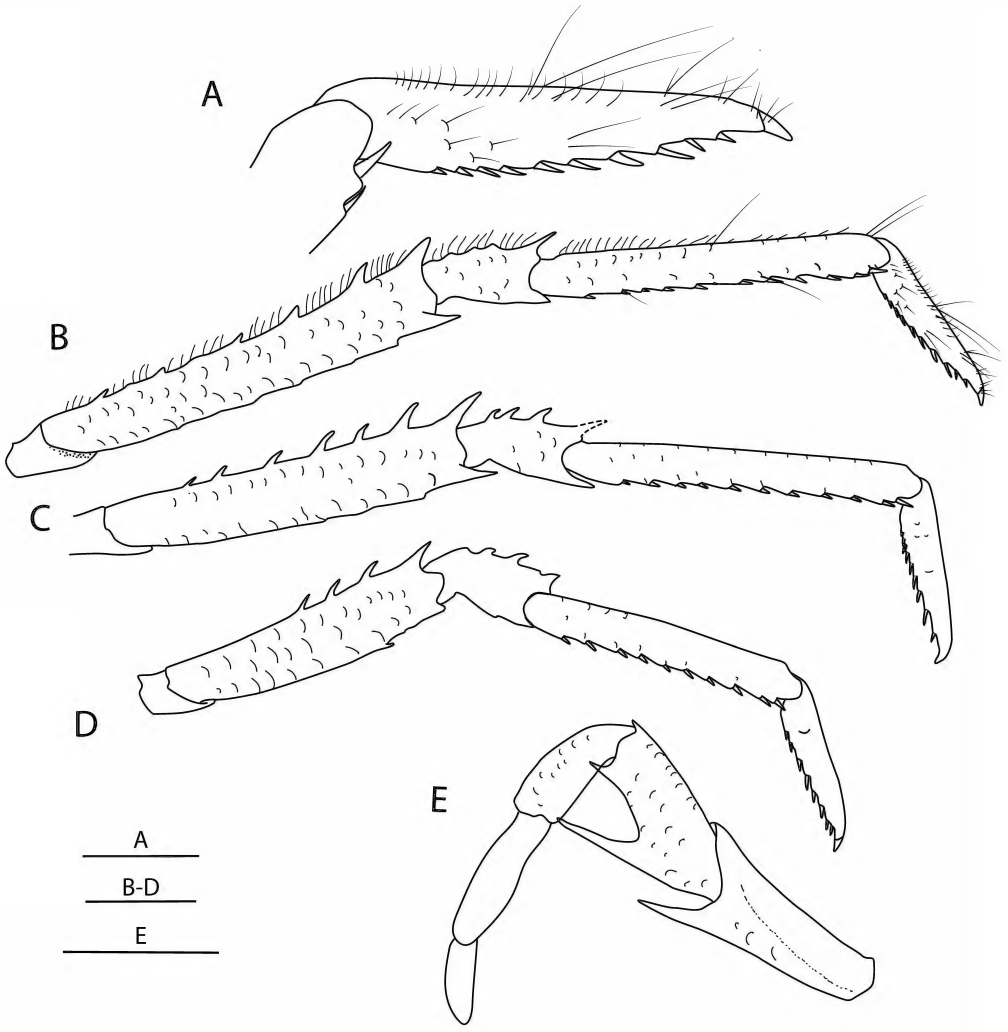


Figure 9. *Munida jurunjurun* sp. nov., holotype, ovigerous female cl 14.7 mm, pcl 9 mm (WAM C78561): A, right P2 dactylus, lateral view; B, right P2, lateral view; C, right P3, lateral view; D, right P4, lateral view; E, left maxilliped 3, lateral view. Scale A = 1 mm, B–E = 2 mm.

***Munida leeuwin* sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:6D615718-C84B-416F-891A-4D9FABFB7592

Figures 10, 11

Munida sp. MoV 5176. — Poore et al., 2008: 20: unnumbered colour fig. (lower right) (south-western Australia, 101–100 m).

Type material. Holotype. WAM C78562, male (cl 8.1 mm, pcl 5.3 mm), Western Australia, Barrow Island, 20° 59.082' S, 114° 54.42' E to 20° 59.67' S, 114° 54.54' E, 100–101 m, SS10/2005/170, 13 December 2005.

Paratypes (all Western Australia). WAM C78563, 1 ovigerous female (cl 7.2 mm, pcl 5 mm), 7 females (cl 6.0 mm, pcl 3.8 mm to cl 8.5 mm, pcl 5.5 mm), 7 males (cl 6.3 mm, pcl 3.8 mm to cl 9.1 mm, pcl 6.2 mm), collected with holotype; NMV J55046, 1 male (cl 8.7 mm, pcl 5.9 mm), 1 ovigerous female (cl 7.9 mm, pcl 5.2 mm), collected with holotype; NMV J55100, 2 ovigerous females (cl 7.7 mm, pcl 5.0 mm; cl 7.8 mm, pcl 5.1 mm), 1 female (cl 7.8 mm, 5.0 mm), collected with holotype; NMV J56100, 1 juvenile (cl 4.4 mm, pcl 3.0 mm), 1 ovigerous female (broken rostrum; pcl 4.8 mm), Imperieuse L23 transect, 18° 27.612' S, 120° 08.682' E to 18° 27.72' S, 120° 08.682' E, 80–81 m, SS05/2007/82, 16 June 2007.

Description. Carapace. Length 1.1 × greatest width, widest at midlength. Dorsal surface with main transverse ridges mostly uninterrupted, without secondary transverse striae between main ridges; ridges and striae lined with short, non-iridescent setae and few long iridescent setae. Gastric region with 5 or 6 pairs of epigastric spines, longest pair behind supraocular spines, with median row of 2 or 3 small spines behind rostrum. Hepatic region with 3 or 4 spines on dorsal surface; parahepatic spines present. Anterior part of branchial region between cervical groove and postcervical groove with 3 ridges and 1 or 2 small spines; 1 postcervical spine; posterior part of branchial region with 4 or 5 main transverse ridges (excluding posterodorsal ridge) and few shorter secondary striae between main ridges. Cardiac region with 3 main transverse ridges. Intestinal region without striae; posterodorsal ridge distinct, without secondary stria. Frontal margin inclined posteriorly at 115° from midline. Lateral margin slightly convex; anterolateral spines parallel, horizontal, not reaching sinus between rostrum and supraocular spine; hepatic marginal spine shorter than anterolateral spine; branchial margin with 5 spines. Rostrum spiniform, slightly sinuous in profile, length 0.5 × pcl; supraocular spine 0.3 × length of rostrum. Epistomial ridge curved, ending anterior to antennal gland; mesial protuberance distinct.

Thoracic sternum. Sternital surface smooth, sternite 4 with few long striae. Sternite 3 0.4 width of sternite 4; midlength of sternal plastron (sternites 4–7) 0.7 width of sternite 7. Sternite 4 anterior margin truncate, entirely contiguous with sternite 3.

Abdomen. Somite 2 without spines. Somites 2–4 each with 2 or 3 uninterrupted striae behind anterior ridge and striae at lateral margins. Somite 6 posteromedian margin almost straight. Telson with numerous transverse squamae; greatest width 2.0 × median length; anterolateral margin concave.

Eye. Maximum corneal diameter 0.35 × distance between anterolateral spines.

Antennule. Basal article (distal spines excluded) not overreaching corneae; distolateral and distomesial spines subequal; 2 lateral spines, proximal smaller, longer lateral spine exceeding distal spines.

Antenna. Article 1 with distomesial spine reaching midlength of article 2. Article 2 distomesial spine slightly overreaching distal margin of article 3; distolateral spine almost reaching distal margin of article 3. Article 3 unarmed or with small distolateral spine. Article 4 unarmed.

Maxilliped 3. Ischium 1.6 × merus length, with distal flexor spine. Merus with 3 well-developed spines on flexor margin; extensor margin with small distal spine.

P1. length 3.1–4.4 pcl (males), 2.8–3.0 pcl (females), with dense covering of iridescent setae on inner margins of merus (without plumose setae), merus 1.3–1.4 (males), 1.0–1.1 (females) × pcl, with row of 5 subtriangular spines on dorsal and mesial margin; distomesial spine not reaching midlength of carpus. Carpus 0.3–0.4 × merus length, length 1.9 (males), 2.0–2.4 (females) × width, with spines along mesial margin. Propodus 1.6–1.7 (males), 1.4 (females) × merus length; fingers 0.4–0.6 (males), 0.5–0.6 (females) × total propodus length; pollex with row of small spines along outer margin; dactylus with 3 small spines on outer margin.

P2–4. Moderately long and slender, with scales on lateral surfaces of meri; extensor margin with plumose setae and iridescent setae. P2 length 2.1–2.6 × pcl; merus as long as carapace, length 6.4 × height, 3.4 × carpus length and 1.3 × propodus length; extensor margin spinose; flexor margin with acute ridges, 1 or 2 spines and well-developed distal spine; carpus with 4 small extensor spines, distal spine on extensor and flexor margin; propodus length 7 × height, with 10–14 movable flexor spines; dactylus compressed, almost straight, 0.7–0.9 × propodus length, length 6–7 × height, flexor margin with 7–12 spines, unarmed along distal 1/3. End of P2 carpus not reaching end of P1 merus. P3 with similar spination and article proportions as P2; merus slightly shorter than P2 merus (0.8); propodus and dactylus as long as those of P2. P4 length 0.8 × P2 length; merus 0.6–0.7 × pcl, 0.9 × P3 merus length; merocarpal articulation almost reaching marginal hepatic spine of carapace.

Genetic data. COI and 16S; see Table 1.

Etymology. Named after the Leeuwin current which flows off the west coast of Australia; used as a noun in apposition.

Remarks. *Munida leeuwin* sp. nov. is most similar to *M. roshanei* Tirmizi, 1966, *M. janetae* Tirmizi and Javed, 1992, and *M. arabica* Tirmizi and Javed, 1992, described from the western Indian Ocean. These three species are very similar to each other and have been distinguished by the length of the pereopod 1 chela, the ratio of the length of the fingers to the propodus palm, and the shape of sternite 3. In his key, Baba (2005) characterises *M. janetae* as having cheliped fingers that are distinctly longer than the palm, while the fingers are shorter than the palm in *M. roshanei* and *M. arabica*. In *M. leeuwin* sp. nov., the fingers are usually as long as the palm but are occasionally longer or shorter than the palm (0.4–0.6 × propodus length). We tentatively describe this species as new based on a combination of subtle differences from the aforementioned species and significant molecular divergence from material we identify as *M. roshanei*. In *M. leeuwin* sp. nov., the dactlyli of P2–4 are slender and

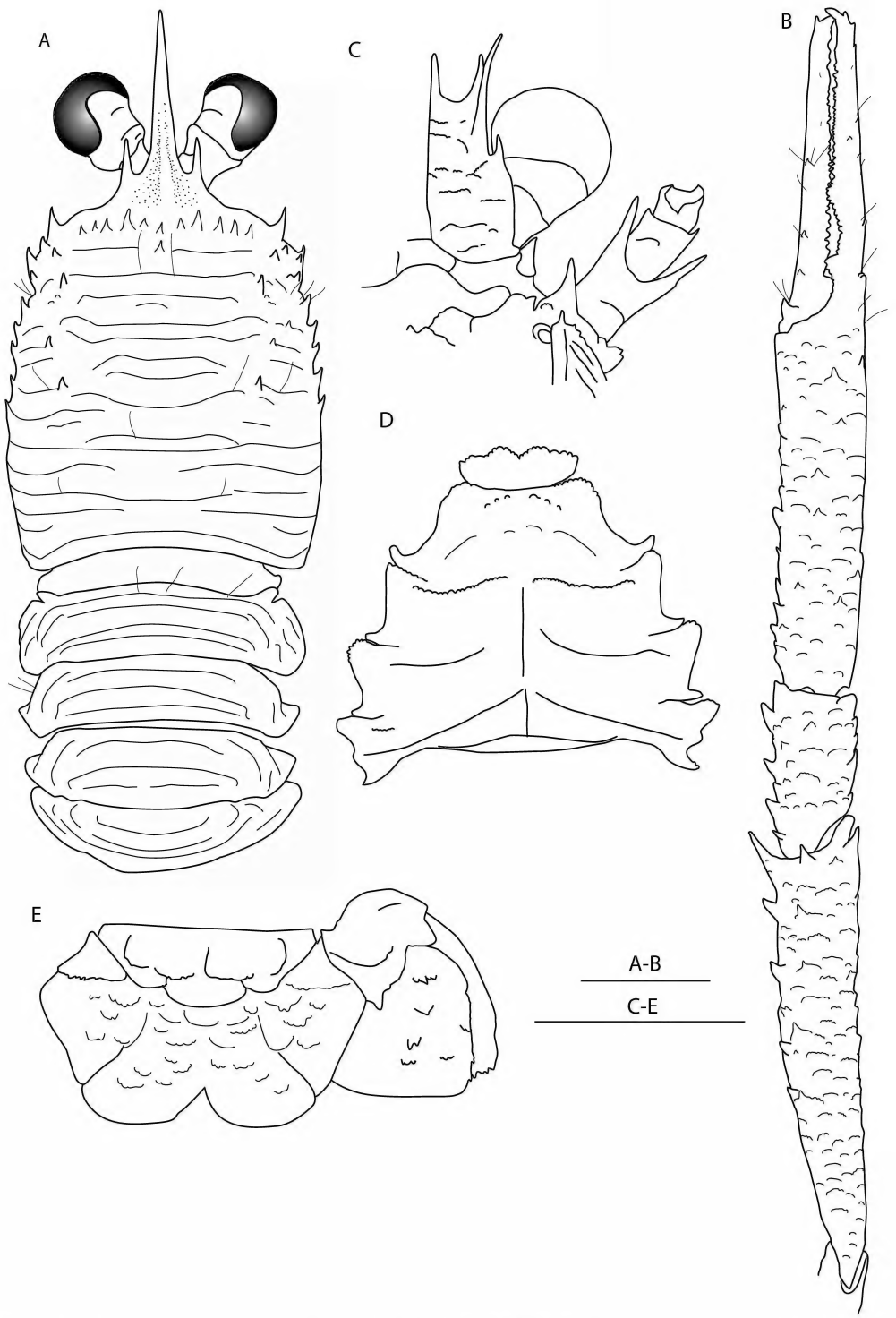


Figure 10. *Munida leeuwin* sp. nov., holotype, male cl 8.1 mm, pcl 5.3 mm (WAM C78562): A, carapace and abdomen, dorsal view; B, right chela, dorsal view; C, left antenna and antennule, ventral view; D, sternum; E, abdominal somite 6, telson and right uropod. Scale: A–E = 2 mm.

unarmed on the distal one-third of the flexor margin, with the ultimate spine closer to the penultimate spine than the unguis. This differs from *M. janetae* in which the dactyli have spines regularly arranged along the entire flexor margin (Tirmizi and Javed, 1992). Illustrations of *M. arabica* show the dactyli to be similar to those of *M. leeuwin* sp. nov., but *M. arabica* can be distinguished by the presence of distal spines on antennal article 4, which are always absent in *M. leeuwin* sp. nov. The type description of *M. roshanei* lacks a description or illustration of the dactyli, as does that of Lewinsohm (1969) for nearby Red Sea specimens. Specimens identified as *M. roshanei* from the Phillipines (Baba, 1988) and Australia (present study), however, have the dactyli with spines regularly arranged along the entire flexor margin. Although the spination of the P2–4 dactyli of the type material of *M. roshanei* remains to be confirmed, given the brevity of the original description and without access to the type, we fully describe *M. leeuwin* as new to improve the taxonomy of this difficult group.

The genetic sequences of *M. leeuwin* are highly divergent from all other species analysed. Despite their morphological similarities, *M. leeuwin* and our specimens of *M. roshanei* are divergent by 12% in COI.

Distribution. Presently known only from off Western Australia, 658–754 m.

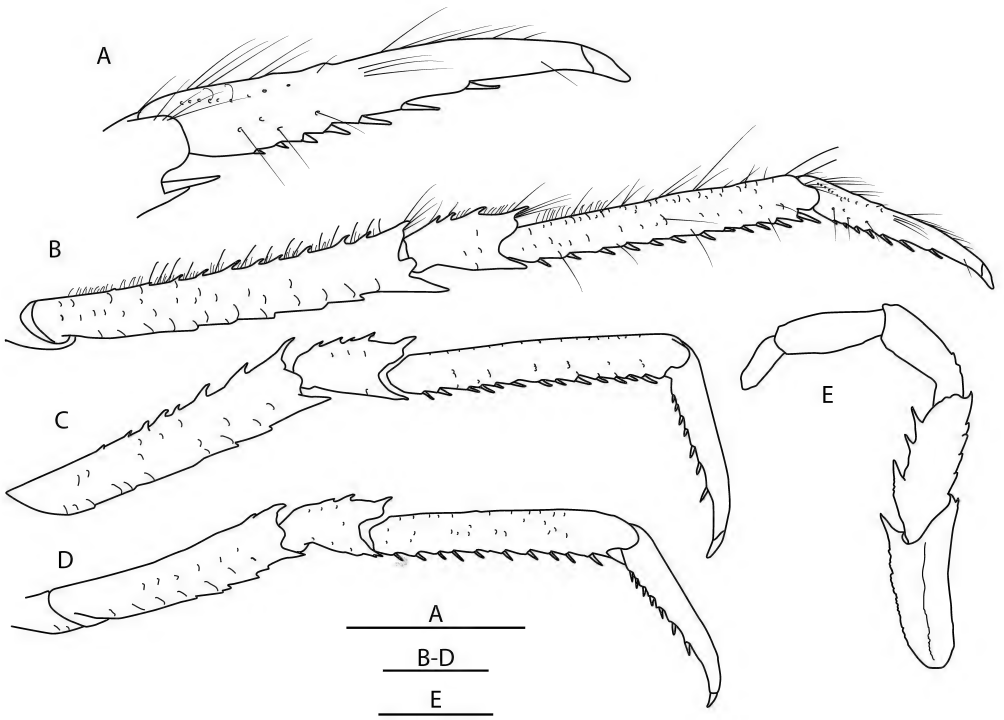


Figure 11. *Munida leeuwin* sp. nov., holotype, male cl 8.1 mm, pcl 5.3 mm (WAM C78562): A, right P2 dactylus, lateral view; B, right P2, lateral view; C, right P3, lateral view; D, right P4, lateral view; E, left maxilliped 3, lateral view. Scale A–E = 1 mm.

***Munida lutruwita* sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:14904374-57EC-4548-A4D7-ACA713F712C9

Figures 3E, 12, 13

Munida cf. *manqingae*. — Farrelly and Ahyong, 2019: 13, 55, fig. 99.

Type material. Holotype: NMV J67481, ovigerous female (cl 11.7 mm, pcl 7.8 mm), Tasmania, south of Hobart, Z39 Seamount, 44° 23.346' S, 147° 16.376' E, 2040 m, TT 01/2008/J2-387-003, 25 December 2008.

Paratypes (all Tasmania): NMV J67474, 2 ovigerous females (cl 9.5 mm, pcl 7.1 mm; cl 9.6 mm, pcl 7.4 mm), Z39 Seamount, 44° 23.32' S, 147° 15.349' E, 1599 m, TT 01/2008/J2-387-023, 26 December 2008; NMV J67475, 2 damaged ovigerous females (cl 10.6 mm, pcl 7.3 mm; cl 11.2 mm , pcl 7.9 mm), Z39 Seamount, 44° 22.994' S, 147° 15.09' E, 1893 m, TT 01/2008/J2-387-008, 25 December 2008; NMV J67480, 1 ovigerous female (cl 11.5 mm, pcl 7.9 mm), Z39 Seamount, 44° 23.295' S, 147° 15.348' E, 1616 m, TT 01/2008/J2-387-022, 26 December 2008; NMV J67472, 1 male (abdomen missing; cl 10.9 mm, pcl 6.3 mm), Z39 Seamount, 44° 23.345'S 147° 16.277'E, 1990–2004 m, TT 01/2008/J2-387-004, 25 December 2008.

Other material examined. AM P103229, 1 ovigerous female (cl 14.3 mm, pcl 10.6 mm), Great Australian Bight, 35° 22.627' S, 132° 19.166' E, 1689–1784 m, from crevice in dead coral, IN2015-C01-042, 6 November 2015.

Description. Carapace. As long as greatest width, widest at midlength. Dorsal surface with main transverse ridges mostly uninterrupted, without secondary transverse striae between main ridges; ridges and striae lined with short, non-iridescent setae. Gastric region with 3 pairs of epigastric spines and 1 or 2 small additional spines, without median row of spines behind rostrum. Hepatic region without spines on dorsal surface. Anterior part of branchial region between cervical groove and postcervical groove with 2 or 3 short tuberculate ridges and often 1 small spine anteriorly; posterior part of branchial region with 5 transverse ridges (excluding posterodorsal ridge). Cardiac region with 2 main transverse ridges. Intestinal region without striae; posterodorsal ridge distinct, without secondary stria. Frontal margin strongly oblique, inclined posteriorly at 115° from midline. Lateral margin slightly convex; anterolateral spine very small, far from reaching sinus between rostrum and supraocular spine; hepatic marginal spine slightly smaller than anterolateral spine; branchial margin with 5 spines. Rostrum spiniform, 0.5 × pcl; supraocular spine 0.25 × length of rostrum, exceeding eyes. Epistomial ridge straight ending at antennal gland; mesial protuberance distinct.

Thoracic sternum. Sternal suface smooth, sternite 4 with only few striae. Sternite 3 0.4 × width of sternite 4. Sterinte 4 anterior margin triangular, narrowly contiguous with sternite 3. Midlength of sternal plastron (sternites 4–7) 0.5 × width of sternite 7.

Abdomen. Somites smooth without spines, distinct ridges or striae. Somite 6 posteromedian margin slightly concave. Telson with few striae; greatest width 1.2 × median length; anterolateral margin weakly concave.

Eye. Maximum corneal diameter 0.18 × distance between anterolateral spines.

Antennule. Basal article (distal spines excluded) overreaching corneae; distolateral spine much longer than distomesial spine; 2 lateral spines, proximal smaller, longer lateral spine not reaching end of distolateral spines.

Antenna. Article 1 distomesial spine almost reaching distal margin of article 2. Article 2 distomesial spine reaching distal margin of article 3; distolateral spine not reaching midlength of article 3. Articles 3 and 4 unarmed.

Maxilliped 3. Ischium 1.9 × merus length, without flexor distal spine. Merus with large median spine and distal spine on flexor margin; extensor margin without distal spine.

P1. Length 2.4–3.2 × pcl, covered in rows of short plumose setae. Merus length 0.9–1.1 × pcl, with row of 2 large spines and 2 small spines on dorsal margin, 1 strong spine on dorsolateral margin, and 4 spines on mesial margin, distomesial spine not reaching midlength of carpus. Carpus 0.5 × merus length, length 3.0 × width, with 6 spines along mesial margin. Propodus 1.3 × merus length, palm with row of 3 or 4 spines on dorsal surface of palm, fingers 0.4–0.5 × total propodus length, without spines on outer margins.

P2–4. Long and slender, with few small scales on lateral sides of meri and carpi; extensor margin with short plumose setae and few longer setae. P2 1.8–2.3 × pcl; merus 0.7–0.8 × pcl, length 8.0 × width, 3.0 × carpus length and 1.5 × propodus length, extensor margin with 5–7 spines, flexor margin with 3 spines and well-developed distal spine; carpus extensor margin with spine at midlength and distal end, flexor margin with distal spine; propodus length about 8 × height, with 5 movable flexor spines on flexor margin; dactylus gently curved distally, 0.6–0.7 × propodus length, length about 7 × height, extensor margin densely lined with stiff short setae on distal half, flexor margin armed along entire length with 12–14 movable spines including spine at base of unguis. End of P2 carpus not reaching end of P1 merus. P3 with similar spination and article proportions as P2; merus 0.9 × P2 merus length, propodus and dactylus as long as those of P2. P4 length 0.7–0.8 × P2 length; merus length 0.3–0.5 × pcl; propodus and dactylus similar in length to those of P3; merocarpal articulation reaching hepatic marginal spine carapace.

Egg diameter. 0.65 mm.

Colour in life. Carapace pink anteriorly fading to white at posterior, abdominal somite 2 white, somites 3–6 pink. P1 and P2–4 white.

Genetic data. COI and 16S; see Table 1.

Etymology. Named *lutruwita*, the original name of Tasmania in *palawa kani*, the language of the Tasmanian Aboriginal people, with the approval of the Tasmanian Aboriginal Centre; used as a noun in apposition.

Remarks. *Munida lutruwita* sp. nov. is very close to *M. manqingae* Liu, Lin and Huang, 2013, described from a single female specimen collected from hydrothermal vent fields at 2218 m in the south-western Indian Ocean. The spination of the antenna and antennule is identical between the two species, but the new species differs from *M. manqingae* in the following:

- the anterior branchial surface of *M. lutruwita* is rugose, with 2 or 3 rows of small tubercles and a small spine anteriorly, but smooth in *M. manqingae*.

- the P2 dactylus has 12–14 movable flexor spines in *M. lutruwita*, but only 10 in *M. manqingae*.

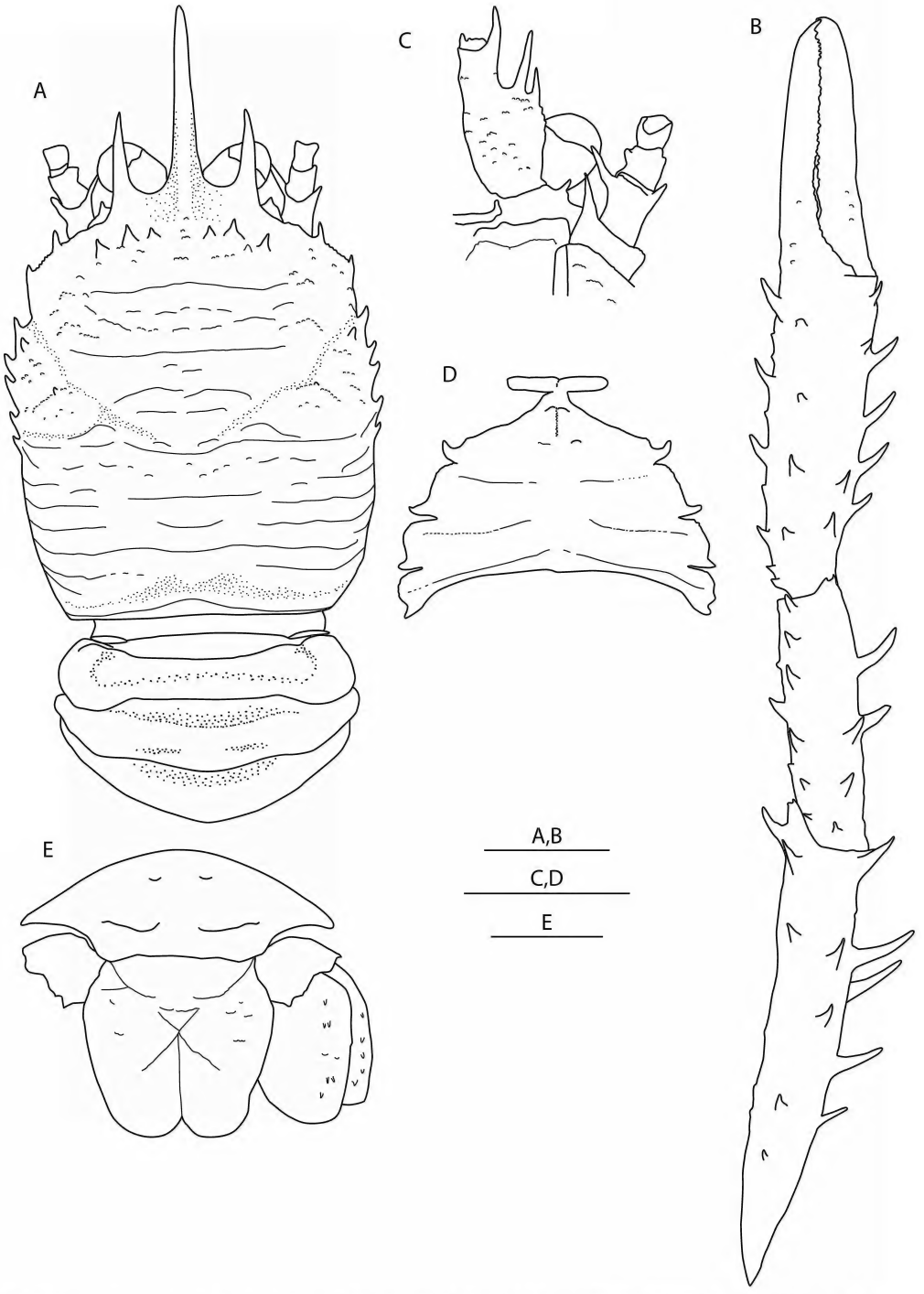


Figure 12. *Munida lutruwita* sp. nov., holotype, ovigerous female, cl 11.7 mm, pcl 7.8 mm (NMV J67481): A, carapace and abdomen, dorsal view; B, right chela, dorsal view; C, right antenna and antennule, ventral view; D, sternum; E, telson. Scale: A–B = 1 mm, C–E = 2 mm.

Munida lutruwita is also very similar to *Munida magniantennulata* Baba and Türkay, 1992, described from hydrothermal vents in the Lau Basin near Fiji, and the recently described, *M. alba* Liu, Li and Lin, 2020, from the Eastern Pacific Rise. Differences between the three species are as follows:

- the antennal article 1 mesial spine reaches the end of article 2 in *M. lutruwita* and *M. alba*, but does not reach as far as the midpoint of article 2 in *M. magniantennulata*.

- the supraocular spines are parallel or slightly convergent, overreaching the eyes in *M. lutruwita*, while in *M. magniantennulata* and *M. alba,* the suproacular spines are slightly divergent and do not overreach the eyes.

- the frontal margins of the carapace are oblique in *M. lutruwita* and *M. alba* rather than near-transverse in *M. magniantennulata*.

- *M. lutruwita* and *M. magniantennulata* further differ from *M. alba* in the presence of the distal flexor spine on the maxilliped 3 merus (absent in *M. alba*) and unarmed outer margin of the cheliped pollex (spinose in *M. alba*).

Distribution. Off southern Tasmania and the Great Australian Bight, 1599–2040 m.

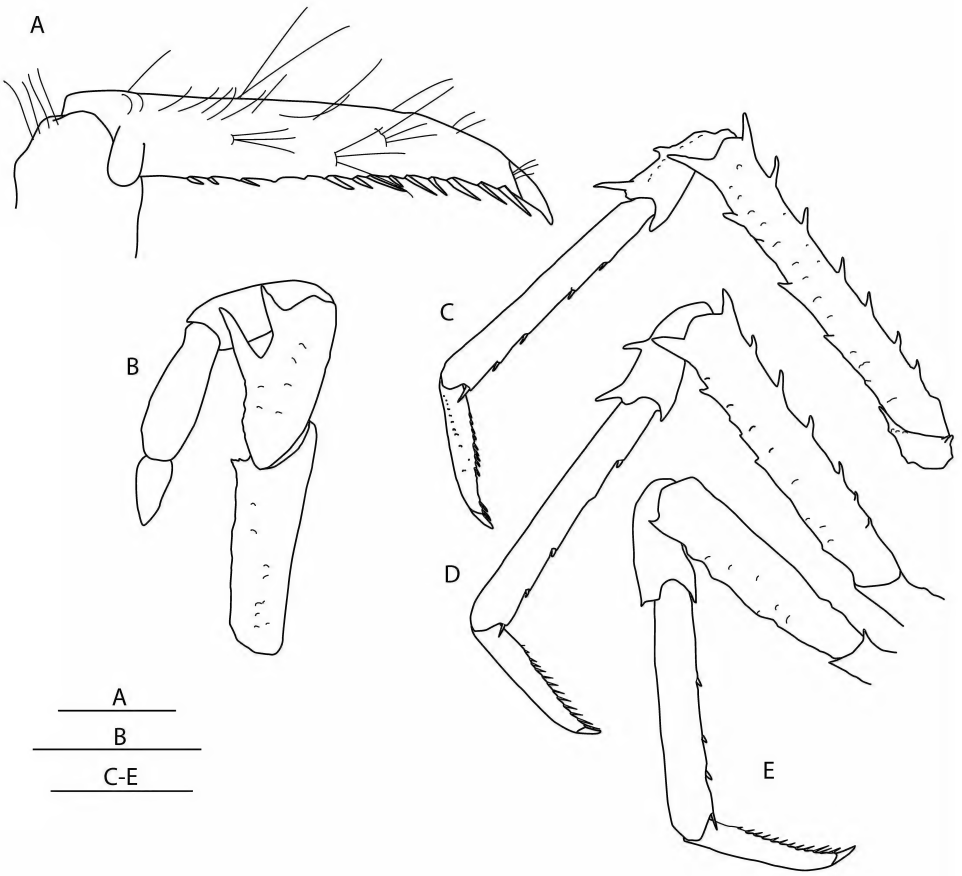


Figure 13. *Munida lutruwita* sp. nov., holotype ovigerous female, cl 11.7 mm, pcl 7.8 mm (NMV J67481): A, right P2 dactylus, lateral view; B, left P2, lateral view; C, left P3, lateral view; D, left P4, lateral view; E, left maxilliped 3, lateral view. Scale = 1 mm.

Munida maatijadakurnaaku sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:354E2119-60D1-498B-9595-32D05B1968BF

Figures 14, 15

Munida aff. *rubiesi* Macpherson, 1991. — Poore et al., 2008.

Type material. Holotype: WAM C78564, male (rostrum broken; pcl 9.0 mm), Western Australia, south-west of Kalbarri, 27° 56.106' S 113° 4.86' E to 27° 56.646' S 113° 5.28' E, 417–428 m, beam trawl, SS10/2005/98, 4 December 2005.

Description. Carapace. Length 1.2 × greatest width, widest at midlength. Dorsal surface with numerous uninterrupted transverse ridges and secondary transverse striae between main ridges; ridges and striae lined with short, non-iridescent setae and scattered long setae. Gastric region with 4 pairs of epigastric spines, longest pair behind supraocular spines. Hepatic region with short scales; parahepatic spine present. Anterior part of branchial region between cervical groove and postcervical groove with dorsal spine and 5 or 6 main ridges; 1 postcervical spine; posterior part of branchial region with 8 main transverse ridges (excluding posterodorsal ridge) and 5 secondary striae laterally between main ridges. Cardiac region with 5 main transverse ridges. Intestinal region with 2 transverse ridges, posterodorsal ridge distinct, with secondary stria. Frontal margin inclined posteriorly at 106° from midline. Lateral margins slightly convex; anterolateral spine slightly divergent, horizontal, overreaching sinus between rostrum and supraocular spine; hepatic marginal spine distinctly smaller than anterolateral spine; branchial margin with 5 spines. Rostrum broken; supraocular spines 0.4 × pcl, exceeding eyes. Epistomial ridge straight ending slightly anterior to antennal gland; mesial protuberance distinct.

Thoracic sternum. Sternal surface smooth, sternites 4 and 5 with few short striae. Sternite 3 0.4 × width of sternite 4; median length of sternal plastron (sternites 4–7) 0.7 × width of sternite 7. Sternite 4 anterior margin subtriangular, narrowly contiguous with sternite 3.

Abdomen. Somite 2 with 5 pairs of spines on anterior transverse ridge. Somites 2–4 each with 5 or 6 uninterrupted striae behind anterior ridge. Somite 6 posteromedian marginslightly convex, posterolateral margins slightly produced. Telson with numerous transverse squamae; greatest width 1.6 × median length; anterolateral margin slightly concave.

Eye. Maximum corneal diameter 0.4 × distance between anterolateral spines.

Antennule. Basal article (distal spines excluded) overreaching corneae; 2 long, subequal distal spines; 2 lateral spines, proximal smaller, distolateral spine not exceeding distal spines.

Antenna. Article 1 with distomesial spine overreaching distal margin of article 2. Article 2 with strong distomesial spine significantly overreaching distal margin of article 4; distolateral spine reaching distal margin of article 3. Articles 3 and 4 unarmed.

Maxilliped 3. Ischium 1.5 × merus length, with strong flexor distal spine; merus with strong spine on flexor margin and small spine distally, without spine on distal extensor margin.

P1. Length 2.8 × pcl, with long plumose setae and iridescent setae, setae longest on dorsal surfaces. Merus length 1.1 × pcl, with a row of 8 dorsal spines and row of 4 spines on mesial margin; distal spines strong, distomesial spine not reaching midlength of carpus. Carpus 0.4 × merus length, length 1.9 × width. Propodus 1.1 × merus length, fingers 0.6 × total propodus length; pollex with row of 5 spines on lateral margin; dactylus with row of 3 spines on dorsal margin, 5 spines on lateral margin and 1 small subdistal spine.

P2–4. Long, slender, with numerous scales on lateral sides of meri; extensor margins with row of plumose and iridescent setae. P2 length 2.3 × pcl, merus as long as carapace, length about 7 × height, 4.0 × carpus length and 1.9 × propodus length, row of spines on extensor margin, flexor margin row of spines and well-developed distal spine; carpus with 2 small spines and 2 large spines on extensor margin, distal spine on flexor margin; propodus length 5.3 × height, with 9 small movable flexor spines; dactylus compressed, almost straight, as long as propodus length, length 8.6 × height, with 7 movable spines along the flexor margin, distal one-quarter unarmed. P3 with similar spination and article proportions as P2; merus slightly shorter than P2 merus (0.75); propodus and dactylus slightly shorter than those of P2. P4 length 0.6 × P2 length; merus 0.4 × pcl, length 0.6 × P3 merus length; propodus 0.8 and dactylus 0.9 × as long as those of P3.

Etymology. Named *maatijada* for crawling and *kurnaaku* for crayfish/yabbie in Nhanda language at the Nhanda Language Day (2 July 2019) at Bundiyarra-Irra Wanga Language Centre in Geraldton; used as a noun in apposition.

Remarks. Despite the broken rostrum in the holotype, *Munida maatijadakurnaaku* sp. nov. is clearly distinguished by a number of diagnostic characters. It is most similar to *M. aequalis* Ahyong and Poore, 2004, from eastern Australia, which also has long and subequal distal spines on the basal antennular article, a subtriangular sternite 4, slender P2–4 dactyli and similar antennal spination. The two species can be distinguished by:

- the supraocular spines overreach the eyes in *M. maatijadakurnaaku* but do not reach the end of the eyes in *M. aequalis*
- antennal article 2 has the distomesial spine significantly overreaching article 4 in *M. maatijadakurnaaku*, but only slightly overreaching article 4 in *M. aequalis*
- the P2–4 dactyli are as long as their respective propodi in the new species, with only the distal one-quarter unarmed, rather than slightly shorter than the propodus and unarmed on the distal one-third in *M. aequalis*.

Distribution. Known only from Western Australia, 417–428 m.

Munida agave Macpherson and Baba, 1993

Figures 16A

Munida agave Macpherson and Baba, 1993: 387, figs 1, 2 (type locality: Philippines). — Baba et al., 2008: 84. — Baba et al., 2009: 139, fig. 115.

Material examined. Western Australia: NMV J56008, 1 female (cl 11.6 mm, pcl 10.4 mm), Broome L25 transect, 16° 45.156' S,

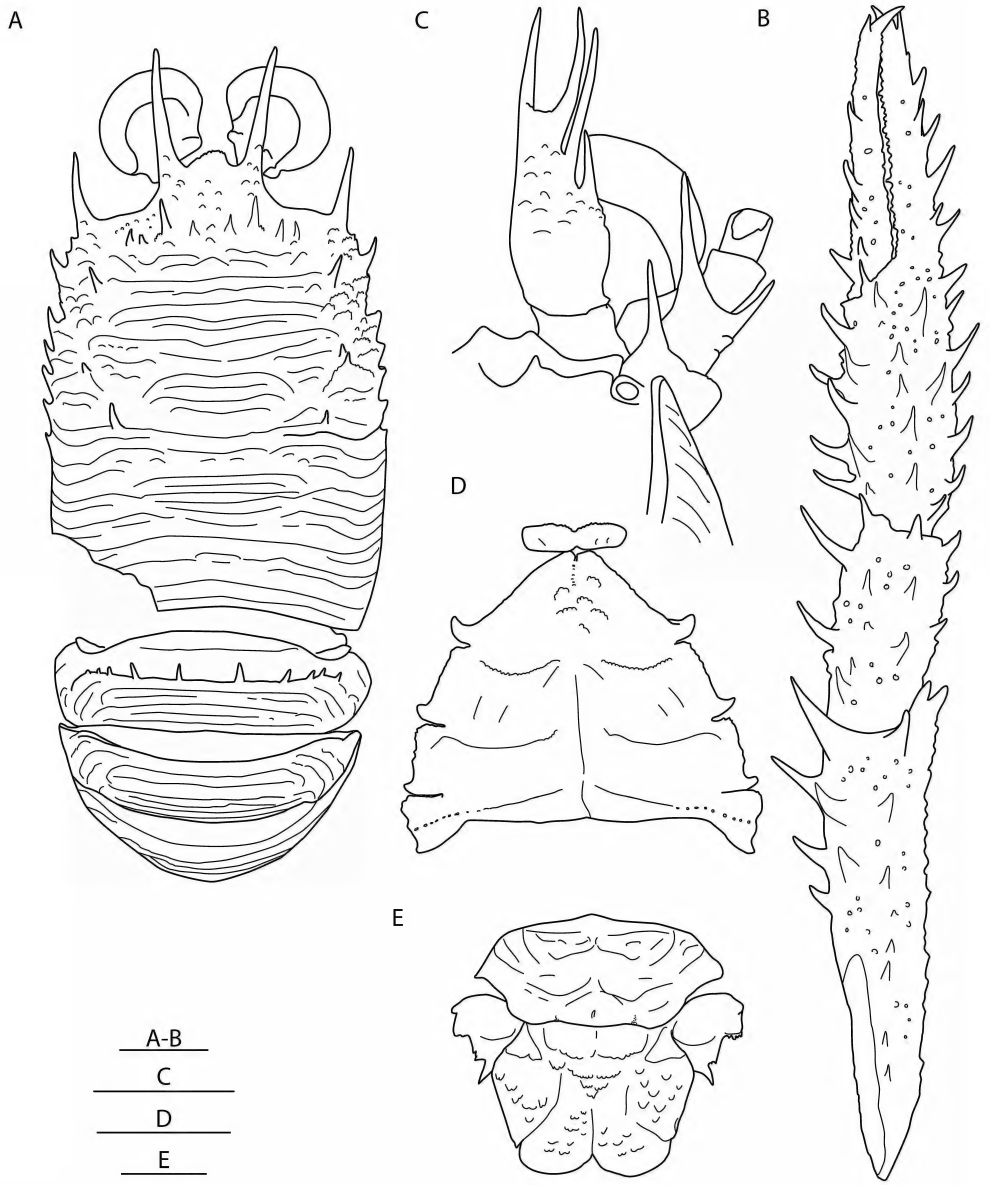


Figure 14. *Munida maatijadakurnaaku* sp. nov., holotype, 1 male with missing rostrum, pcl 9.0 mm (WAM C78564): A, carapace and abdomen, dorsal view; B, right chela, dorsal view; C, right antenna and antennule, ventral view; D, sternum; E, telson. Scale A–E = 2 mm.

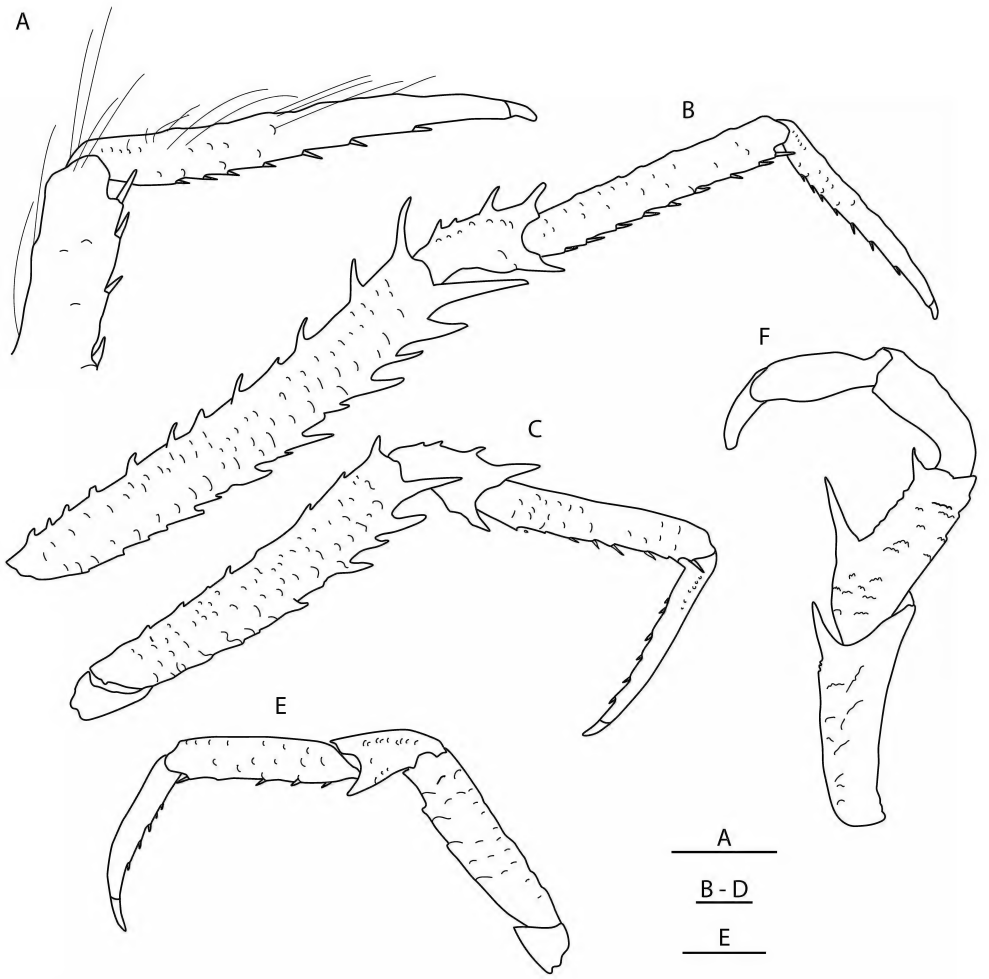


Figure 15. *Munida maatijadakurnaaku* sp. nov., 1 male with missing rostrum, pcl 9.0 mm (WAM C78564): A, right P2 dactylus, lateral view; B, left P2, lateral view; C, left P3, lateral view; D, left P4, lateral view; E, left maxilliped 3, lateral view. Scale: A–E = 1 mm.

121° 02.796' E to 16° 44.592' S, 121° 02.208' E, 100–108 m, SS05/2007/116, 30 June 2007; NMV J56099, Adele L28 transect, 14° 33.732' S, 122° 55.092' E to 14° 33.684' S, 122° 54.906' E, 95–105 m, SS05/2007/161, 4 July 2007.

Colour. Carapace and abdominal somites 2–5 pale orange with orange striae and spines, telson whiteish. Rostrum and supraocular spines orange. P1 and P2–4 pale orange with orange striae.

Genetic data. COI and 16S; see Table 1.

Remarks. This specimen agrees well with the description of the holotype from the Phillipines, having arcuate striae on sternites 3–6 and two pairs of spines on the anterior ridge of abdominal somite 2. This is the first record of the species from Australia.

Distribution. Japan, Philippines, Indonesia, Taiwan, 89–549 m. North-western Australia, 55–108 m.

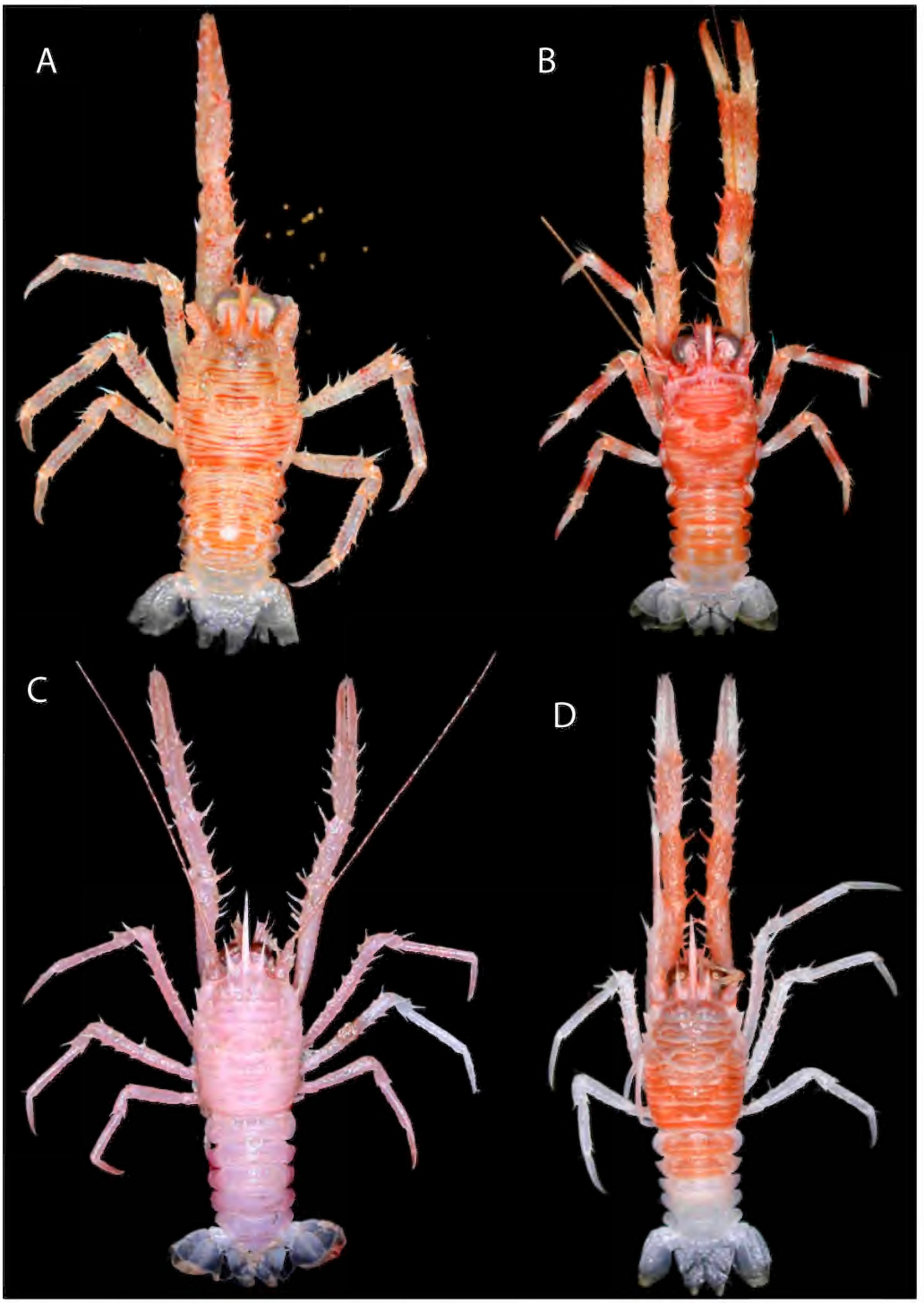


Figure 16. A, *Munida agave* Macpherson and Baba, 1993, female, cl 11.6 mm, pcl 10.4 mm (NMV J56008); B, *Munida armilla* Macpherson, 1994, male, cl 16.1 mm, pcl 10.2 mm (NMV J55081); C–D, *Munida asprosoma* Ahyong and Poore, 2004, male, cl 13.2 mm, pcl 8.0 mm (J55076), ovigerous female, cl 17.4 mm, pcl 10.7 mm (NMV J56016). Photos: K. Gowlett-Holmes.

Munida armilla Macpherson, 1994

Figure 16B

Munida armilla Macpherson, 1994: 446, figs 6, 65 [type locality: New Caledonia]. — Baba et al., 2008: 87. — Macpherson, 2013: 296.

Munida aff. *amathea* — Poore et al., 2008: 20.

Material examined. Western Australia: NMV J55081, 1 male (cl 16.1 mm, pcl 10.2 mm),

Abrolhos, 28° 29.37' S, 113° 25.14' E to 28° 30.06' S, 113° 25.5' E, 416–431 m, SS10/2005/95, 2005.

Colour. Carapace and abdominal somites pink/white with orange/reddish striae and spines. Rostrum white with red tip, supraocular spines red at base and white distally, anterolateral spines red. Walking legs with orange/red bands. Chela with orange bands.

Genetic data. Not available.

Remarks. This single specimen differs slightly from the type material of *M. armilla* Macpherson, 1994. In our specimen the basal article of the antennule has subequal distal spines while in the holotype the distomesial spine is slightly shorter than the distolateral. In our specimen the carapace has interupted striae while the holotype has numerous scales. This is the first record of the species from Australia.

Distribution. New Caledonia, Matthew and Hunter Islands, Tuscaroa Bank, Tonga, French Polynesia (Tarava seamounts, Tuamoto and Society Archipelagos), 233–710 m. Western Australia, 416–431 m.

Munida asprosoma Ahyong and Poore, 2004

Figure 16C–D

Munida asprosoma Ahyong and Poore, 2004: 20, fig. 3 (type locality: east of Broken Bay, New South Wales, Australia). — Baba et al., 2008: 87. — Baba et al., 2009: 146, figs 123–126. — Poore et al., 2011: pl. 16D. — McEnnulty et al., 2011: app. 1.

Material examined. Western Australia: NMV J56016, 2 ovigerous females (cl 16.3 mm, pcl 10.2 mm; cl 17.4 mm, pcl 10.7 mm), Mermaid L24 transect, 16° 38.064' S, 119° 09.216' E to 16° 38.766' S, 119° 08.034' E, 983–993 m, SS05/2007/68, 17 June 2007;

NMV J56096, 1 female (cl 13.9 mm, pcl 8.3 mm), 1 juvenile (cl 10.3 mm, pcl 6.0 mm), Mermaid L24 transect, 16° 44.286' S, 119° 15.042' E to 16° 43.794' S, 119° 15.48' E, 693–698 m, SS05/2007/70, 17 June 2007; NMV J56393, 2 females (pcl 6.7–8.1 mm; #B, #A), 1 male (pcl 5.0 mm; #C), Leveque L27 transect, 14° 33.06' S, 121° 15.366' E to 14° 33.588' S, 121° 16.56' E, 1021–1023 m, SS05/2007/155, 3 June 2007; NMV J57258, 1 ovigerous female (cl 20.6 mm, pcl 12.7 mm), SS05/2007/155; NMV J55077, 1 male (cl 20.4 mm, pcl 12.2 mm), Perth Canyon, 31° 57.9' S, 115° 06.3' E to 31° 56.982' S, 115° 07.08' E, 928–1170 m, SS10/2005/73, 30 November 2005; NMV J55078, 4 ovigerous females (cl 18.7 mm, pcl 10.7 mm to cl 22.1 mm, pcl 13.6 mm), 19 females (cl 14.4 mm, pcl 8.6 mm to cl 23.5 mm, pcl 14.5 mm), 11 males (cl 12.4 mm, pcl 7.4 mm to cl 26.5 mm, pcl 15.9 mm), SS10/2005/73; NMV J55076, 3 males (cl 13.2 mm, pcl 8.0 mm to cl 21.5 mm, pcl 12.8 mm), Abrolhos, 29° 00.594' S, 113° 42.78' E to 29° 01.512' S, 113° 43.32' E, 700–704 m, SS10/2005/85, 2 December 2005; NMV J55079, 1 female (cl 16.9 mm, pcl 10.4 mm), 5 males (cl 15.9 mm, pcl 9.6 mm to cl 26.1 mm, pcl 16.1 mm), SS10/2005/85.

Colour. Carapace, abdomen, chela and P2–4 pale pink. Reddish on distal portion of fingers, antenna and posterior margin of carapace. One specimen photographed is different in colour from the other two photographed specimens. This specimen was collected from the Abrolhos station at ~700 m (male, cl 13.2 mm, pcl 8.0 mm, NMV J55076). The carapace is white with orange on the striae and abdominal somites 2–3, P2–4 are white, the chelae are orange with white fingers.

Genetic data. COI; see Table 1.

Remarks. The present specimens of *M. asprosoma* from Western Australia accord well in most respects with those from eastern Australia (Ahyong and Poore, 2004). Three juveniles (NMV J56393; pcl 5.0–8.1 mm), however, differ from adults in having lesser developed abdominal spination: the median pair of spines on the anterior ridge of abdominal somite 2 is well developed but spines laterad are either incipent or minute, and the anterior ridge of somite 3 is unarmed. Thus, the diagnostic spination of the abdominal somites may not be fully developed in juveniles and care should be taken when identifying small specimens.

The COI sequences of *M. asprosoma* were only 1.3% divergent from *Munida hoda* Macpherson, Rodríguez-Flores and Machordom, 2017, from Mozambique. Intraspecific divergence between the three specimens sequenced here was 0.3–0.6%. These species share a number of morphological characters including: the presence of 5 spines on the branchial lateral margins of the carapace, strongly oblique frontal carapace margins, absence of secondary striae between the widely spaced primary striae, spines along the anterior ridge of the abdominal somite 2, large eyes, and the distomesial spine of the antennular article 1 shorter than the distolateral spine. They can easily be distinguished by the presence of spines on abdominal somite 3 in adults of *M. asprosoma*, and the flexor spination of the P2 dactyli, with 7–9 spines in *M. asprosoma* and only 4 spines in *M. hoda*. One of the specimens photographed had a different colour pattern from the others (NMV J55076, male pcl 8.0 mm; see above) but we could find no other morphological characters to distinguish this specimen from the others. Similarly, Baba et al. (2009) showed a number of distinct colour morphs of *M. asprosoma* from Taiwan, not dissimilar to the variation reported here, and in some cases different from that of the holotype (Poore et al. 2011: pl. 16D).

Distribution. Eastern Australia (New South Wales and Queensland), Vanuatu, Taiwan, 495–1802 m. Western Australia, 700–1170 m.

Munida babai Tirmizi and Javed, 1976

Munida babai Tirmizi and Javed, 1976: 81–85, fig. 1, 2 (type locality: off Natal, South Africa). — Baba et al., 2008: 88. — McEnnulty et al., 2011: app. 1.

Material examined. Western Australia: NMV J55044, 2 males (cl 7.7 mm, pcl 5.1 mm to cl 7.8 mm, pcl 5.3 mm), Ningaloo North, 21° 58.704' S, 113° 49.2' E to 21° 59.052' S, 113° 49.2' E, 170–177 m, SS10/2005/152, 10 December 2005; NMV J55041, 2 males (cl 7.8 mm, pcl 5.3 mm; cl 9.2 mm, pcl 5.9 mm), Ningaloo North, 21° 59.172' S, 113° 49.2' E to 21° 59.79' S, 113° 49.14' E, 165–166 m, SS10/2005/153,

11 December 2005; NMV J55042, 3 females (cl 6.0 mm, pcl 3.8 mm; cl 6.1 mm, pcl 4.0 mm), 4 males (cl 7.7 mm, pcl 5.0 mm; cl 8.1 mm, pcl 5.7 mm), Barrow Island, 20° 59.082' S, 114° 54.42' E to 20° 59.67' S, 114° 54.54' E, 100–101 m, SS10/2005/170, 13 December 2005.

Genetic data. CO1; see Table 1.

Remarks. Originally described from off South Africa (off Natal), *M. babai* has subsequently been reported from shelf depths across the Indian Ocean as far east as Hong Kong (Baba, 1988). It can be distinguished by the presence of spines on the anterior margin of abdominal somite 4 and very short supraocular spines. As noted by Baba (1988), the number of spines on the abdominal somites is variable. We found abdominal somite 2 with 5–9 spines, somite 3 with 2–5, and somite 4 with 2–5 spines. The P2 dactylus is 0.75 the length of the propodus in Australian specimens compared to 0.64 for the type (based on Tirmizi and Javed, 1976: fig. 2D), and 0.84 for the Albatross material from Hong Kong and the Phillipines (Baba, 1988). This is the first record of the species from Australia.

Distribution. South Africa, Madagascar, Hong Kong, Malaysia, 70–456 m. Western Australia, 100–177 m.

Munida benguela de Saint Laurent and Macpherson, 1988

Munida benguela de Saint Laurent and Macpherson, 1988: 106, figs 1, 2a, 2c, 3a, 3d, 3f–i (type locality: south of Namibia). — Baba et al., 2008: 89.

Material examined. Western Australia: NMV J56405, 1 male (damaged; cl 11.6 mm, pcl 8.2 mm), SS05/2007/176, Kulumburu L29 transect, 13° 13.482' S 123° 23.742' E to 13° 13.338' S 123° 23.286' E, 392 m, 5 July 2007.

Genetic data. Not available.

Remarks. Although this specimen is damaged, most diagnostic characters are evident. In *M. benguela,* the P2 dactylus has 6–8 spines with the ultimate being distant from the unguis. Similarly, our specimen has 8 spines and is unarmed on the distal one-third. In *M. benguela,* the fixed finger of the chela has at least 4 spines on the lateral margin which agrees with our specimen. However, our specimen lacks any spines on the mesial margin of the moveable finger while *M. benguela* has a subdistal spine and an additional 2–4 spines on the mesial margin.

Distribution. South African coast between S Namibia and Natal, and Madagascar; 352–1000 m. North-west Australia, 392 m.

Munida compacta Macpherson, 1997

Figure 17A–C

Munida compacta Macpherson, 1997: 605–606, fig. 2 (type locality: Kei Islands, Indonesia). — Baba et al., 2008: 90.

Munida andamanica. — Poore et al., 2008: 19. — McEnnulty et al., 2011: app. 1, 2.

Material examined. Queensland. AM P89035, 2 ovigerous females (pcl 11.7–13.5 mm), east of Cape York, 10° 29.810' S, 144° 01.380' E, 596 m, RV *Franklin*, FR0688-02, 20 August 1988. Western Australia. AM P72138, 1 ovigerous female (cl 26.5 mm, pcl 19.7 mm), 240 km north-west of Port Hedland, 18° 06' S, 117° 45' E, 500 m, RV *Soela*, S02/82/31, coll. J. Paxton, 7 April 1982; NMV J56402, 1 male (cl 14 mm, pcl 7.0 mm), Onslow L19 transect, 20° 07.962' S, 114° 58.71' E to 20° 07.584' S, 114° 58.416' E, 415–470 m, SS05/2007/15, 11 June 2007; NMV J56409, 4 females (cl 18.8 mm, pcl 11.6 mm; cl 26.5 mm, pcl 18.0 mm), Dampier L20 transect, 19° 43.548' S, 115° 20.604' E to 19° 43.764' S, 115° 21.144' E, 415–428 m, SS05/2007/28, 12 June 2007; NMV J56414, 1 male (cl 14.5 mm, pcl 7.8 mm), SS05/2007/28; NMV J56408, 1 male (cl 17.9 mm, pcl 11.3 mm), Hedland L22 transect, 18° 34.194' S, 117° 27.864' E to 18° 34.062' S, 117° 28.626' E, 401–405 m, SS05/2007/52, 14 June 2007; NMV J55266, 1 female (cl 13.5 mm, pcl 8.5 mm), Imperieuse L23 transect, 17° 21.492' S, 118° 57.312' E to 17° 20.88' S, 118° 56.802' E, 437–446 m, SS05/2007/56, 15 June 2007; NMV J56412, 2 males (cl 24.7 mm, pcl 16.5 mm; cl 25.0 mm, pcl 16.6 mm), SS05/2007/56; NMV J56411, 3 males (cl 15.7 mm, pcl 9.5 mm to cl 18.0 mm, pcl 11.2 mm), 1 ovigerous female (cl 27.3 mm, pcl 18.1 mm), Imperieuse L23 transect, 17° 31.734' S, 118° 50.61' E to 17° 32.508' S, 118° 50.352' E, 403–407 m, SS05/2007/57, 15 June 2007; NMV J56426, 1 female (cl 14.4 mm, pcl 7.6 mm), SS05/2007/57; NMV J55260, 3 ovigerous females (cl 23.9 mm, pcl 16.0 mm to cl 25.9 mm, pcl 24.0 mm), Imperieuse L23 west transect, 17° 31.044' S, 118° 51.162' E to 17° 31.716' S, 118° 50.742' E, 405–406 m, SS05/2007/64, 16 June 2007; NMV J55265, 1 male (cl 12.4 mm, pcl 7.5 mm), SS05/2007/64; NMV J55990, 1 female (18.9 mm, pcl 13.4 mm), 1 juvenile (cl 9.5 mm, pcl 8.4 mm), SS05/2007/64; NMV J56406, 1 male (cl 11.5, pcl 10.5 mm), SS05/2007/64; NMV J56410, 1 ovigerous female (cl 24.5 mm, pcl 16.7 mm), Leveque L27 transect, 14° 50.814' S, 121° 26.436' E to 14° 50.94' S, 121° 28.164' E, 382–401 m, SS05/2007/102, 26 June 2007; NMV J56080, 8 males (cl 19.9 mm, pcl 14.7 mm to cl 26.7 mm, pcl 16.9 mm), 3 females (cl 21.9 mm, pcl 14.8 mm to cl 25.7 mm, pcl 18.3 mm), Leveque L27 transect, 14° 51.198' S, 121° 25.878' E to 14° 50.724' S, 121° 27.012' E, 396–403 m, SS05/2007/144, 2 July 2007; NMV J56081, 2 females (cl 20.6 mm, pcl 12.6 mm; cl 22.4 mm, pcl 15.1 mm), 1 juvenile (cl 14.9 mm, pcl 9.2 mm), Ashmore L30 transect, 12° 28.884' S, 123° 25.062' E to 12° 29.958' S, 123° 25.002' E, 397–405 m, SS05/2007/189, 6 July 2007; NMV J55994, 4 ovigerous females (cl 22.4 mm, pcl 15.1 mm to cl 23.5 mm, pcl 15.6 mm), 1 female (cl 24.1 mm, pcl 16.3 mm), 3 males (cl 19.6 mm, pcl 12.9 mm to cl 24.4 mm, pcl 16.3 mm), Ashmore L30 transect, 12° 31.77' S, 123° 25.638' E to 12° 30.828' S, 123° 25.362' E, 401–404 m, SS05/2007/192, 6 July 2007; NMV J55051, 1 female (cl 14.4, pcl 9.0 mm), Barrow Island, 21° 00.402' S, 114° 22.86' E to 21° 00.042' S, 114° 22.5' E, 399–408 m, SS10/2005/172, 13 December 2005.

Colour. Carapace and abdominal somites 2–4 pale orange/pink. Rostrum red, supraocular spines white or red and white on distal half. P1 pale orange/pink with white fingers, P2–4 pale orange on meri and carpi, white on propodi, dactyli white with red tips.

Genetic data. COI and 16S; see Table 1.

Remarks. *Munida compacta* is very close to *M. rubridigitalis* Baba, 1994, and *M. julumunyju* sp. nov. from eastern and western Australia, respectively, and *M. rhodonia*, from New Caledonia. These species can be distinguished by:

- the dactylus of P2 is similar in length (0.8–1.0) to the propodus in *M. compacta* and distinctly shorter (0.8) in *M. rhodonia*

- chelipeds with well-developed spines on the dorsal face of the palm in *M. compacta*, which are instead very small in *M. rhodonia*.

While the length of the distomesial spine of the P1 merus was used to differentiate these species (Baba, 1997), we found

Figure 17. A–C, *Munida compacta* Macpherson, 1997, female, dorsal view and lateral (NMV J56409), female 18.9 mm, pcl 13.4 mm (NMV J55990); D, *Munida endeavourae* Poore and Ahyong, 2004, ovigerous female, cl 21.7 mm, pcl 13.9 mm (NMV J55052); E, *Munida gordoae* Macpherson, 1994 (NMV J56420). Photos: K. Gowlett-Holmes, CSIRO.

that that the length of this spine varied in our specimens of *M. compacta* and did not always overreach the midlength of the carpus. Also, the P2 dactylus in *M. compacta* is described as clearly shorter than the propodus, but in our specimens, the P2 dactylus was 0.8–1.0 times the propodus length.

The sequences of *M. compacta* from north-western Australia and *M. rhodonia* from New Caledonia were 1.2% divergent for COI and 0.2% divergent for 16S.

The present specimens represent the first confirmed records of *M. compacta* from Australia.

Distribution. Indonesia, Kei Islands, 246–694 m. Queensland and Western Australia, 397–470 m.

Munida compressa Baba, 1988

Munida compressa Baba, 1988: 91, figs 33, 34 (type locality: Moluccas, Indonesia). — Baba et al., 2008: 91. — Baba et al., 2009: 152, figs 130–134. — Poore et al., 2011: pl. 16H (colour).

Material examined. Western Australia: NMV J55980, 1 male (cl 21.2 mm, pcl 13.0 mm), Kulumburu L29 transect, 13° 13.482' S, 123° 23.742' E to 13° 13.338' S, 123° 23.286' E, 392 m, SS05/2007/176, 5 July 2007; NMV J55981, 4 males (cl 12.0 mm, pcl 8.2 mm; cl 18.6 mm, pcl 12.1 mm), Ashmore L30 transect, 12° 28.884' S, 123° 25.062' E to 12° 29.958' S, 123° 25.002' E, 397–405 m, SS05/2007/189, 6 July 2007.

Genetic data. 16S and COI; see Table 1.

Remarks. This is the first record of the *Munida compressa* from Australia. Sequences from our material and a specimen from the Solomon Islands (Machordom and Macpherson, 2004) were 0.2% divergent for COI and invariant for 16S.

Distribution. Indonesia, Japan, Taiwan, Arafura Sea, 180–668 m. North-west Australia, 392–405 m.

Munida distiza Macpherson, 1994

Munida distiza Macpherson, 1994: 459, figs 14, 68, 69 (type locality: New Caledonia). — Baba et al., 2008: 93. — Macpherson, 2013: 300.

Material examined. NMV J56487, 1 ovigerous female (cl 20.3 mm, pcl 12.6 mm), 1 male (cl 18.7 mm, pcl 12.4 mm), Barrow L1 transect, 21° 00.816' S, 114° 39.15' E to 21° 00.78' S, 114° 38.898' E, 258–271 m, SS05/2007/11, 10 June 2007.

Genetic data. COI and 16S; see Table 1.

Remarks. COI sequences from this material were 4–5% divergent from sequences of *Munida distiza* Macpherson, 1994, from New Caledonia. However, we could not find any distinguishing morphological characters.

Distribution. Philippines, New Caledonia, Loyalty Islands, Matthew and Hunter Islands, French Polynesia, 150–540 m. North-west Australia, 258–271 m.

Munida endeavourae Ahyong and Poore, 2004

Figure 17D

Munida endeavourae Ahyong and Poore, 2004: 26, fig. 5 (type locality: south-east of Green Cape, New South Wales, Australia). — Baba et al., 2008: 94. — Yaldwyn and Webber, 2011: 211. — Farrelly and Ahyong, 2019: 13, 54. — Yan et al. 2020: 2, tab. 1.

Munida grievae Vereshchaka, 2005: 140, fig. 3A–F (type locality: Bay of Plenty, New Zealand).

Munida sp. MoV 5199. — Poore et al., 2008: 21, unnumbered figure (lower right). —McEnnulty et al., 2011, app. 1, 2.

Material examined. Western Australia: NMV J55052, 1 ovigerous female (cl 21.7 mm, pcl 13.9 mm), Albany, 35° 26.046' S, 118° 21.06' E to 35° 26.19' S, 118° 20.64' E, 912–922 m, SS10/2005/28, 23 November 2005. Tasmania: MV J59312, 1 specimen, Cascade Plateau, 43° 49.706' S, 150° 29.999' E, 1061 m, TT 01/2008/J2-390-015, 4 January 2009; MV J59310, 1 specimen, Hill off St. Helens, 41° 14.349' S, 148° 49.293' E, 1309 m, TT 01/2008/J2-389-006, 1 January 2009.

Colour. Carapace, abdomen, chela and P2–4 pink. Eggs red.

Genetic data. COI and 16S; see Table 1.

Remarks. Poore et al. (2008) and McEnnulty et al. (2011) recorded *M. endeavourae* from south-western Australia as "*Munida* sp. MoV 5199"; the present record is the first confirmation of the species from the area.

Distribution. South-eastern Australia from south-east of Green Cape to Tasmania, 620–1700 m. South-western Australia, 912–922 m

Munida gordoae Macpherson, 1994

Figure. 17E

Munida gordoae Macpherson, 1994: 469, fig. 18 (type locality: Chesterfield Islands). — Baba et al., 2008: 97.

Munida aff. *volantis*. — Poore et al., 2008, 20, unnumbered fig. — McEnnulty et al., 2011: 26, app. 1, 2.

Material examined. Western Australia: NMV J56420, 3 ovigerous females (cl 5.7 mm, pcl 3.5 mm to cl 8.2 mm, pcl 5.3 mm), 8 males (cl 5.1 mm, pcl 2.9 mm to cl 8.1 mm, pcl 6.1 mm), 2 juveniles (cl 4.8 mm, pcl 3.1 mm; cl 5.1 mm, pcl 3.2 mm), Imperieuse L23 east transect, 17° 35.706' S, 118° 58.902' E to 17° 35.346' S, 118° 58.794' E, 140–108 m, SS05/2007/62, 16 June 2007; NMV J55087, 3 males (cl 10.0 mm, pcl 6.3 mm to cl 11.2 mm, pcl 7.2 mm), Two Rocks, 31° 37.452' S, 115° 00.24' E to 31° 37.71' S, 115° 00.18' E, 205–210 m, SS10/2005/11, 19 November 2005; NMV J55085, 1 male (cl 12.0 mm, pcl 6.3 mm), Perth Canyon, 31° 55.26' S, 115° 12.12' E to 31° 55.446' S, 115° 11.76' E, 194–232 m, SS10/2005/69, 29 November 2005; NMV J55088, 1 female (cl 11.0 mm, pcl 6.3 mm), Abrolhos, 28° 59.328' S, 113° 47.04' E to 28° 59.784' S, 113° 47.28' E, 180–183 m, SS10/2005/91, 3 December 2005; NMV J55086, 5 ovigerous females (cl 7.3 mm, pcl 4.8 mm to cl 11.2 mm, pcl 7.4 mm), 1 damaged male, Kalbarri, 27° 55.716' S, 113° 08.28' E to 27° 56.022' S, 113° 08.64' E, 252–253 m, SS10/2005/99, 4 December 2005.

Colour. Carapace and abdominal somite 2–3 pink and orange patterning. Abdominal somite 4–6 with white markings. Rostrum and supraocular spines orange/pink. Chela and P2-4 orange/red with white bands.

Genetic data. COI and 16S.

Remarks. These are the first records of *M. gordoae* from Australia. Sequence divergence between our north-western Australian specimens of *M. gordoae* and those from New Caledonia was only 0.2% for COI and 0.4% for 16S.

Distribution. New Caledonia, Loyalty Islands, Matthew and Hunter Islands, and Chesterfield Islands, Vanuatu, Fiji, 80–500 m. Western Australia, 180–232 m.

Munida gracilis Henderson, 1885

Figure 18

Munida gracilis Henderson, 1885: 412 (type locality: New Zealand, 38° 50' S, 169° 20' E). — Baba et al., 2008: 97. — Yaldwyn and Webber, 2011: 212. — Yan et al. 2020: 2, tab. 1.

Munida chydaea Ahyong and Poore, 2004: 24, fig. 4 (type locality: east of Brush Island, New South Wales, Australia). — Poore, 2004: 234, fig. 64b. — Baba, 2005: 260. **Syn. nov.**

Munida disgrega Baba, 2005: 103, figs 40, 41 (east of Victoria, Australia). — Poore et al., 2008: 19. — McEnnulty et al., 2011: app. 1. **Syn. nov.**

Material examined. South Australia: SAM C7658, 1 ovigerous female (cl 32.3 mm, pcl 18.5 mm), 1 damaged specimen (cl 18.5 mm, pcl 10.6 mm), Great Australian Bight, 33° 27.09' S, 130° 41.19' E, 500 m, BPZ 2010/500, 2010.

Western Australia: NMV J55107, 2 females (cl 24.8 mm, pcl 13.7 mm; cl 26.1 mm, pcl 15.5 mm), 3 males (cl 20.6 mm, pcl 11.2 mm to cl 21.9 mm, pcl 12.1 mm), Bald Island, 35° 14.022' S, 118° 39.84' E to 35° 13.674' S, 118° 40.5' E, 710–728 m, SS10/2005/32, 2005; NMV J55106, 6 females (cl 11.4 mm, pcl 6.3 mm to cl 25.4 mm, pcl 14.3 mm), 10 males (cl 12.4 mm, pcl 7.4 mm to cl 24.0 mm, pcl 13.6 mm), Bald Island, 35° 14.022' S, 118° 39.84' E to 35° 13.674' S, 118° 40.5' E, 710–728 m, SS10/2005/32, 23 November 2005; NMV J55083, 3 males (cl 27.9 mm, pcl 19.5 mm to cl 47.8 mm, pcl 34.9 mm), Pt Hillier, 35° 22.902' S, 117° 12.42' E to 35° 22.902' S, 117° 12.42' E, 539 m, SS10/2005/19, 2005; NMV J55080, 1 female (pcl 7.9 mm), Albany, 35° 22.29' S, 118° 19.98' E to 35° 22.644' S, 118° 19.26' E, 685–695 m, SS10/2005/27, 2005; NMV J55084, 16 females (cl 20.9 mm, pcl 11.9 mm to cl 36.6 mm, pcl 19.6 mm), 19 males (cl 14.3 mm, pcl 9.0 mm to cl 30.2 mm, pcl 17.9 mm), Albany, 35° 22.14' S, 118° 20.1' E to 35° 22.518' S, 118° 19.32' E, 676–680 m, SS10/2005/29, 2005; NMV J55082, 1 female (cl 9.1 mm, pcl 7.0 mm), 2 males (cl 17.4 mm, pcl 7.8 mm; cl 15.1 mm, pcl 9.9 mm), Bald Island, 35° 12.81' S, 118° 39.06' E to 35° 12.24' S, 118° 40.14' E, 408–431 m, SS10/2005/34, 2005.

New Zealand: NIWA 53772, 1 female (cl 23.3 mm, pcl 15.8 mm), 44° 09.47' S, 174° 33.32' W to 44° 09.48' S, 174° 33.56' W, 520–650 m, TAN0905/103, 26 June 2009; NIWA 54087, 1 ovigerous female (cl 21.0 mm, pcl 12.2 mm), Diamondhead Peak B, Andes Seamounts, 44° 08.97' S, 174° 45.41' W to 44° 09.02' S, 174° 45.63' W, 519–609 m, TAN0905/113, 27 June 2009; NIWA 54108, 1 female (cl 24.4 mm, pcl 13.9 mm), Diamondhead Peak B, Andes Seamounts, 44° 08.99' S, 174° 46.09' W to 44° 09.01' S, 174° 46.3' W, 830–900 m, TAN0905/114, 27 June 2009; NIWA 63655, 4 males (pcl 5.4–7.7 mm), Site 3a seamount, Hikurangi Margin, 41° 19.16' S, 176° 11.84' E to 41° 19.28' S, 176° 11.53' E, 495 m, TAN1004/66, 21 April 2010.

Genetic data. CO1 and 16S; see Table 1.

Remarks. *Munida gracilis* is a common species in New Zealand, usually from depths of 300–600 m with a recorded range of about 100–1200 m (Yan et al., 2020), that is morphologically closest to the Australian *Munida chydaea* Ahyong and Poore, 2004. COI sequences of specimens corresponding to *Munida chydaea* Ahyong and Poore, 2004, from south-western Australia, however, were only 0.9–1.0% divergent from *M. gracilis* from New Zealand and 0.2% divergent for 16S. This low level of sequence divergence led us to further examine the morphological distinctions between *M. gracilis* and *M. chydaea*. Ahyong and Poore (2004) distinguished the two species based on the number of anterior

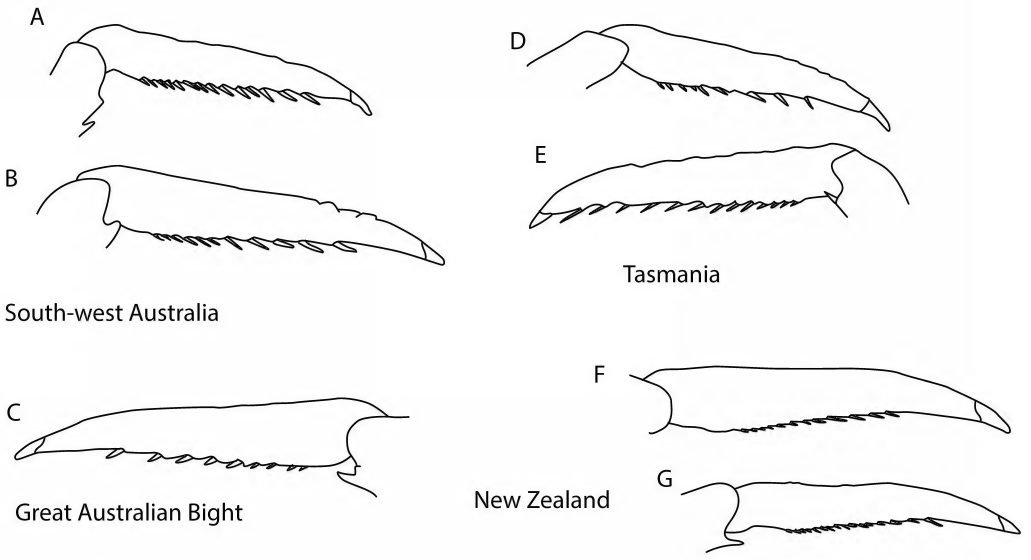


Figure 18. *Munida gracilis* Henderson, 1885. Variation of P2 dactyli. A. female cl 32 mm, 18.3 mm; B. male cl 26.2 mm, pcl 15.5 mm (NMV J55048); C, ovigerous female, cl 32.3 mm, pcl 18.5 mm (SAM C7658); D, male cl 21.2 mm, pcl 11.9 mm (NMV J53574); E, female, cl 30.0 mm (J53574); F, female cl 23.5 mm, pcl 15.8 mm (NIWA 53772); G, ovigerous female, cl 21.0 mm, pcl 12.2 mm (NIWA 54087).

spines on abdominal somite 3 (1 or 2 spines in *M. chydaea*; 4 spines in *M. gracilis*), the length of the unarmed flexor margin of the P2 dactyli (distal one-quarter in *M. chydaea* versus distal one-third in *M. gracilis*), spinules on the outer margin of antennal articles 3 and 4 in *M. chydaea* (absent in *M. gracilis*) and more numerous transverse abdominal striae in *M. chydaea*. Our comparisons between new Australian and New Zealand specimens, however, failed to identify consistent distinguishing features. Although the many specimens examined by Ahyong and Poore (2004), primarily from from eastern Australia, were consistent in the aforementioned features, specimens examined herein from southern Australia (Tasmania, South Australia and Western Australia) and New Zealand exhibit morphological overlap. Thus, the shape and armature of the P2 dactyli in southern Australian specimens is variable, with the flexor margin unarmed on the distal one-fifth to one-third (fig. 21A–E). Similar variation was seen in the eight New Zealand specimens we examined; in most specimens, the distal one-third of the P2 dactylus was unarmed (fig. 21F) but in one ovigerous female (pcl 12.2 mm; NIWA 54087; Fig. 21G), the distal one-quarter was unarmed. Similarly, abdominal somite 3 is variously armed with 2–4 spines, albeit usually 4 in adult New Zealand specimens, and almost always 2 in adult southern Australian specimens. Another character used to distinguish *M. chydaea* was the presence of outer spinules on the third and fourth antennal article, but such spinules were present on all eight of the specimens of *M. gracilis* we examined from New Zealand. Thus, considered as a whole, Australian material is not reliably morphologically separable from New Zealand specimens, and given the minimal divergence between New Zealand and Western Australian sequences, we consider both populations as probably conspecific.

This brings *Munida disgrega* Baba, 2005, to our attention, which was described from 4 small specimens (cl 10.1–13.0 mm) collected from south-eastern Australia and noted as very close to *M. chydaea* and *M. gracilis*. In *M. disgrega*, the flexor margin of the dactylus is unarmed on the distal one-quarter to one-fifth, which is encompassed by the newly observed variation in *M. gracilis* and *M. chydaea*. Other distinguishing features of *M. disgrega*, such as the length of the chela, the lesser striation and broader anterior margin of the thoracic sternum, and proportionately wider eyes apppear to be allometric differences given the small size of the type specimens. Consequently, we cannot reliably distinguish *M. disgrega* from *M. gracilis* or *M. chydaea*

Although we do not have molecular data from eastern Australia (type region of *M. chydaea*), on the basis of the low molecular divergence (between New Zealand and south-western Australian specimens) and morphological variability within southern Australian specimens that encompasses those from New Zealand and eastern Australia, we regard *M. chydaea* and *M. disgrega* as junior synonyms of *M. gracilis*. *Munida gracilis* is closely related to, but clearly distinct from, *M. haswelli,* with 7.6% divergence in COI and 3.3% in 16S.

Distribution. Southern Australia (Sydney to south-western Australia), 146–700 m. New Zealand, 365–610 m.

Munida haswelli Henderson, 1885

Figure 19A

Munida haswelli Henderson, 1885: 411 (type locality: off southern New South Wales, Australia). — Baba et al., 2008: 98. — McEnnulty et al., 2011: app. 1, 2. — Farrelly and Ahyong, 2019: 13, 54, fig. 96.

Material examined. Western Australia: NMV J60017, 2 males (cl 19.5 mm, pcl 12.3 mm; cl 19.6 mm, pcl 12.5 mm), Ashmore L30 transect, 12° 26.058' S, 123° 36.078' E, 125 m, SS05/2007/186, 6 June 2007; NMV J55102, 1 male (cl 12.1 mm, pcl 7.4 mm), Two Rocks, 31° 37.452' S, 115° 00.24' E to 31° 37.71' S, 115° 00.18' E, 205–210 m, SS10/2005/11, 19 November 2005; NMV J55103, 1 male (cl 19.6 mm, pcl 12.8 mm), SS10/2005/11; NMV J55104, 3 ovigerous females (cl 14.0 mm, pcl 9.0 mm to cl 15.4 mm, pcl 10.2 mm), 2 males (cl 11.4 mm, pcl 7.2 mm; cl 16.4 mm, pcl 10.4 mm), Bald Island, 35° 11.442' S, 118° 38.7' E to 35° 11.25' S, 118° 39' E, 147–157 m, SS10/2005/35, 24 November 2005; NMV J55105, 5 ovigerous females (cl 11.5 mm, pcl 7.5 mm to cl 15.2 mm, pcl 8.9 mm), 5 males (cl 12.3 mm, pcl 7.9 mm to cl 16.4 mm, pcl 11.3 mm), Bald Island, 35° 11.406' S, 118° 38.94' E to 35° 11.514' S, 118° 38.76' E, 161–169 m, SS10/2005/38, 24 November 2005; NMV J55108, 4 ovigerous females (cl 14.4 mm, pcl 9.3 mm to cl 16.0 mm, pcl 10.8 mm), 9 females (cl 11.3 mm, pcl 7.7 mm to cl 16.1 mm, pcl 11.2 mm), 18 males (cl 13.6 mm, pcl 9.1 mm; cl 21.4 mm, pcl 14.5 mm), Albany, 35° 21.276' S, 118° 17.94' E to 35° 21.348' S, 118° 17.76' E, 179 m, SS10/2005/47, 25 November 2005; NMV J55109, 4 females (largest with broken rostrum; pcl 6.2–9.5 mm), 3 males (cl 11.9 mm, pcl 7.6 mm; cl 13.9 mm, pcl 9.0 mm), Pointt Hillier, 35° 22.41' S, 117° 11.82' E to 35° 22.404' S, 117° 12.24' E, 195–196 m, SS10/2005/57, 27 November 2005; NMV J55099, 3 ovigerous females (cl 11.2 mm, pcl 7.5 mm to cl 11.5 mm, pcl 7.7 mm), 11 males (one with rhizocephalan externa; cl 8.6 mm, pcl 6.1 mm to cl 11.8 mm, pcl 8.7 mm), Ningaloo North, 21° 59.172' S, 113° 49.2' E to 21° 59.79' S, 113° 49.14' E, 165–166 m, SS10/2005/153, 11 December 2005; NMV J55101, 1 ovigerous female (cl 10.4 mm, pcl 7.2 mm), Ningaloo North, 21° 56.628' S, 113° 50.46' E to 21° 57.09' S, 113° 50.28' E, 132–134 m, SS10/2005/163, 12 December 2005.

Colour. Carapace and somites 2–4 pale orange, somites 5–6 and telson white. Rostrum and supraocular spines orange. Chela orange/pink with red bands on distal half of palm. P2–4 whitish pink with red bands on middle of propodus.

Genetic data. COI and 16S; see Table 1.

Remarks. *Munida haswelli* and *Munida gracilis* are closely related, with 7.6% divergence in COI and 3.3% divergence in 16S.

Distribution. Central New South Wales, south to Victoria, Tasmania, South Australia, the Great Australian Bight and Western Australia, 121–329 m.

Munida heteracantha Ortmann, 1892

Munida heteracantha Ortmann, 1892: 255, pl. 11 fig. 12, 12i, 12k (type locality: Sagami Bay, Japan). — Baba et al., 2008: 99. — Poore et al., 2008: 19. — McEnnulty et al., 2011: app. 1. — Castro, 2011: 16

Munida sp. MoV 5214. — Poore et al., 2008: 21.

Material examined. Western Australia: NMV J55037, ovigerous female (cl 9.4 mm, pcl 6.35 mm), 1 ovigerous female (cl 9.8 mm, pcl 7.2 mm), 4 females (cl 8.3 mm, pcl 5.3 mm to cl 9.3 mm, pcl 6.6 mm), 4 males (cl 6.9 mm, pcl 4.4 mm to cl 10.5 mm, pcl 6.7 mm), 3 juveniles (cl 6.1 mm, pcl 4.1 mm to cl 6.6 mm, pcl 4.5 mm), Ningaloo South,

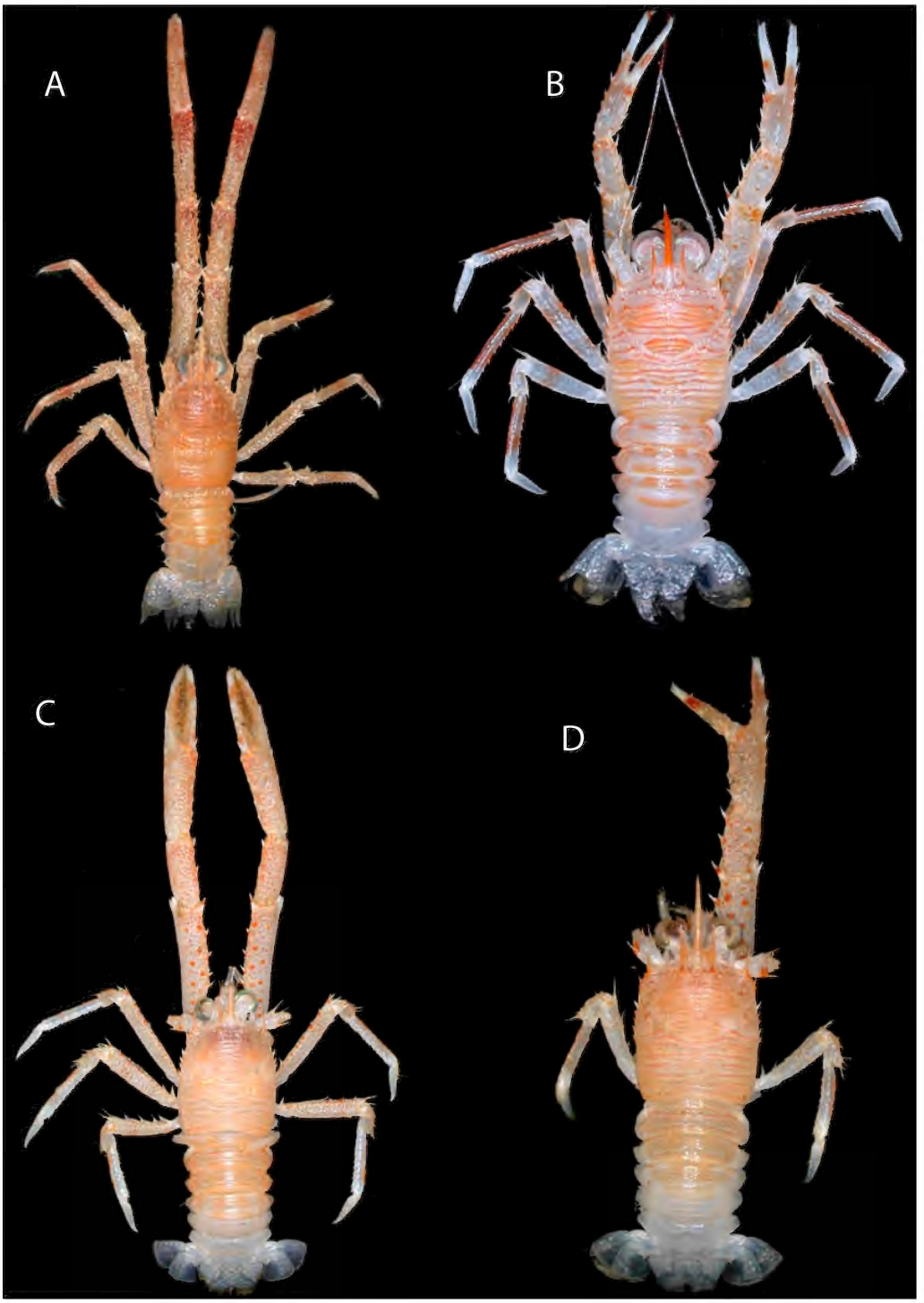


Figure 19. A, *Munida haswelli* Henderson, 1885, male cl 19.55 mm (NMV J55103), pcl 12.81 mm; B–D, *Munida leagora* Macpherson, 1994, 1 juvenile cl 12.2 mm, pcl 7.5 mm (NMV J56018), undetermined specimen (NMV J55999; NMV J56004). Photos: K. Gowlett-Holmes.

22° 04.77' S, 113° 47.76' E to 22° 05.238' S, 113° 47.64' E, 201–206 m, SS10/2005/146, 10 December 2005; NMV J55038, 1 male (cl 10.7, pcl 7.4 mm), 1 female (cl 7.5 mm, pcl 5.0 mm), SS10/2005/146; NMV J55040, 1 male (cl 10.5 mm, pcl 7.0 mm), 1 ovigerous female (cl 9.9 mm, pcl 7.1 mm), 1 female (cl 7.6 mm, pcl 5.2 mm), Ningaloo North, 21° 58.704'S 113° 49.2'E to 21° 59.052'S 113° 49.2'E, 170–177 m, SS10/2005/152, 10 December 2005.

Genetic data. Not available.

Remarks. *Munida heteracantha* Ortmann, 1892 has been recorded widely across the western Pacific, including from Queensland, Australia. Our specimens show some variation from the lectotype from Japan described by Macpherson and Baba (1993). The lectotype has a pair of small parahepatic spines, which are absent in all our material. In most of our specimens the distolateral spine of the basal antennular article is slightly longer than the distomesial spine, while in the lectotype the distal spines are subequal. Macpherson and Baba (1993) noted that some specimens of *M. heteracantha* have 2 small median spines on abdominal somite 3, and half of the specimens here have 1–6 spines. Only three specimens had the P2 attached, and these show the dactyli with 7–8 spines on the flexor margin, compared to only 5 spines in the lectotype.

Munida heteracantha is also similar to *Munida macphersoni* Cabezas, Lin and Chan, 2011, but differs in the length of the supraocular spines, which are very short in *M. heteracantha* (0.34 × rostral length compared to 0.5 in *M. macphersoni*).

Distribution. Japan, Philippines, and Indonesia, off Central Queensland, New Caledonia, Fiji, 100–322 m. South-western Australia, 170–177 m.

Munida leagora Macpherson, 1994.

Figure 19B–D

Munida leagora Macpherson, 1994: 485, figs 26, 76 (type locality: New Caledonia). — Baba et al., 2008: 104.

Material examined. Western Australia: NMV J56004, 1 ovigerous female (cl 13.8 mm, pcl 8.1 mm), 1 male (cl 13.0 mm, pcl 8.0 mm), Leveque L27, 14° 58.362' S, 121° 38.556' E to 14° 57.762' S, 121° 39.264' E, 228–232 m, SS05/2007/143, 2 July 2007; NMV J55999, 5 males (cl 15.7 mm, pcl 9.5 mm to cl 20.2 mm, pcl 12.3 mm), 1 male with bopyrid (cl 14.9 mm, pcl 8.6 mm), 1 ovigerous female (cl 16.5 mm, pcl 10.2 mm), SS05/2007/143; NMV J56018, 1 juvenile (cl 12.2 mm, pcl 7.5 mm), Mermaid L24 east transect, 17° 02.838' S, 119° 39.684' E to 17° 03.708' S, 119° 41.358' E, 424–456 m, SS05/2007/77, 18 June 2007.

Colour. Carapace and abdominal somites 2–4 pale orange, somites 5–6 and telson white. Rostrum and supraocular spines pale orange. P1 and P2–4 meri with orange spots at base of spines and on striae.

Genetic data. COI and 16S; see Table 1.

Remarks. *Munida leagora* was described from New Caledonia, and the present specimens represent the first records of the species from Australia. Our specimens show some minor variation compared to the type description, including the presence of 1 or 2 small spines on the lateral margins of the anterior ridge of abdominal somite 2, and the presence of parahepatic spines in some specimens. *Munida leagora* is very similar to *Munida alia* Baba, 1994, described from a single specimen in Queensland. We compared our specimens of *M. leagora* to the holotype of *M. alia* and confirmed that these species are distinct. In Baba's (2005) key to *Munida*, these two species are separated by the length of the distomesial spine of antennal article 1, which reaches the end of article 2 in *M. alia* and reaches or overreaches the distal end of article 3 in *M. leagora*. In addition, *M. alia* lacks a pair of postcervical spines, which are always present in our specimens of *M. leagora*.

Divergence in COI sequences between specimens of *M. leagora* from north-western Australia and New Caledonia is <0.5%. The wide transverse yellow and purple bands on the carapace described for New Caledonian specimens are absent in all the specimens examined here.

Distribution. New Caledonia, Loyalty Islands, Chesterfield Islands, Vanuatu, Bayonnaise Bank, Fiji and Tonga, 240–610 m. North-west Australia, 232–456 m.

Munida magniantennulata Baba and Türkay, 1992

Figure 20A

Munida magniantennulata Baba and Türkay, 1992: 205, figs 2, 3 (type locality: Lau Basin). — Baba et al., 2008: 105. — Farrelly and Ahyong, 2019: 13, 54. fig. 97.

Not *Munida magniantennulata*. — Baba, 1994a: 12 (=*M. typhle* Macpherson, 1994)

Material examined. New South Wales: NMV J73001, 3 ovigerous females (cl 10.6 mm, pcl 7.2 mm to cl 13.4 mm, pcl 12.5 mm), Central Eastern CMR, 30° 05.862' S, 153° 53.922' E to 30° 07.158' S, 153° 52.47' E, 2429–2518 m, IN2017_v03/086, 5 June 2017.

Colour. Carapace, abdomen, cheliped and P2–4 pink. Eggs red.

Genetic data. Not available.

Remarks. The type specimens of *M. magniantennulata* are described as having the P2 dactylus 0.5–0.6 times propodus length, 6.6 times as long as high, and lined with 10 movable spines. Our specimens have a very similar P2 dactylus, which is 0.6–0.7 times the propodus length, 5–6 times as long as high, with 9–10 movable spines on the flexor margin. The chelipeds of all our specimens lack spines on the outer margin of the fingers or on the dorsal face of the palm, which agrees with the type material. All the specimens have two small tubercle-like spines on abdominal somite 2.

These specimens differ from the holotype in the length of the mesial spine on the first antennal article, which reaches the midlength of article 2 in these specimens but is very short in the holotype.

The specimens recorded by Baba (1994) as *M. magniantennulata* from off central Queensland are referred to *Munida typhle* Macpherson 1994 (see *Remarks* for that species).

Distribution. Lau Basin, 1750–2003 m. Eastern Australia, 2429–2518 m.

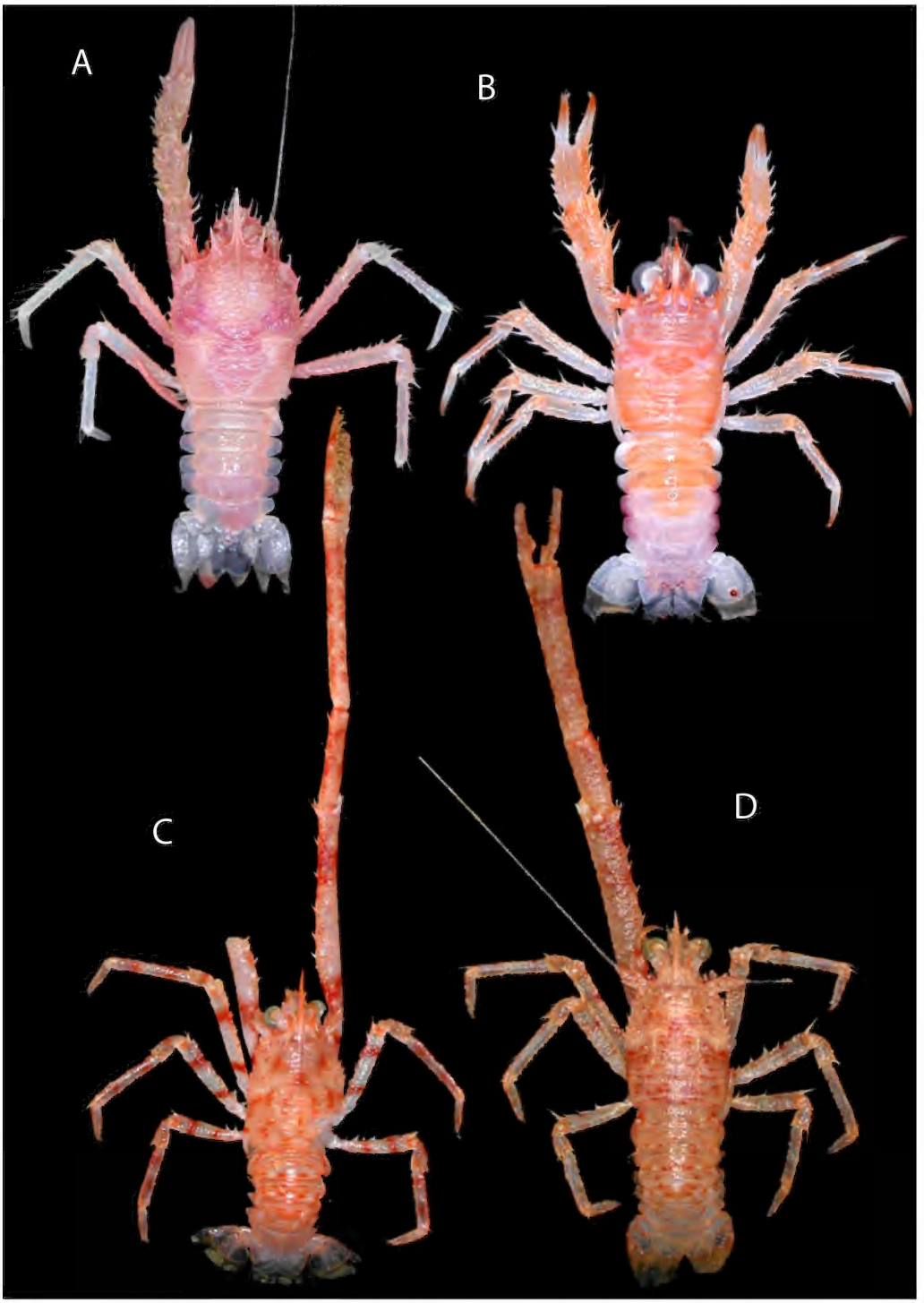


Figure 20. A, *Munida militaris* Henderson, 1885, ovigerous female cl 15.0 mm, pcl 9.4 mm, (NMV J55033); B, *Munida magniantennulata* Baba and Türkay, 1992, ovigerous female (NMV J73001); C, *Munida pectinata* Machordom and Macpherson, 2005, male (NMV J55268); D. *Munida roshanei* Tirmizi, 1966, male 11.1 mm, pcl 7.2 mm (NMV J55261). Photos: K. Gowlett-Holmes, CSIRO.

Munida militaris Henderson, 1885

Figure 20B

Munida militaris Henderson, 1885: 410 (type locality: off Mataku, Fiji Islands). — Baba, 2008: 108 (synonymies, type data). — Baba et al., 2009: 173, figs 153–155 (in part) (Taiwan, 190–1183 m). — Poore et al., 2011: pl. 17E (colour).

Not *Munida militaris* Baba et al., 2009: 173 (in part) (Taiwan) (= *M. lanciaria* Cabezas et al., 2011).

Munida aff. *Rubiesi* — Poore et al., 2008, 20 (part), unnumbered fig.

Munida MoV 5183. — McEnnulty et al., 2011: app. 1, 2.

Material examined. Western Australia: NMV J55033, 1 ovigerous female (cl 15.0 mm, pcl 9.4 mm), 31° 36.528' S 114° 58.86' E to 31° 37.038' S 114° 58.26' E, 329–370 m, SS10/2005/06, 19 November 2005; NMV J55035, 1 ovigerous female (cl 15.0 mm, pcl 10.2 mm), near Abrolhos islands, 28° 29.37' S 113° 25.14' E to 28° 30.06' S 113° 25.5' E, 416–431 m, SS10/2005/95, 4 December 2005.

Genetic data. Not available.

Colour. Carapace and somites 2–4 orange and white, somites 5–6 and telson white. Rostrum and supraocular spines orange on base and tips and white in the middle. Chela white and orange, and orange/red bands on distal half of fingers. P2–4 transparent white/orange with orange/red across the middle of propodus and tips of dactyli.

Remarks. The specimens here agree with the lectotype description of *M. militaris* by Baba and Macpherson (1991). *Munida militaris* closely resembles *M. benguela* de Saint Laurent and Macpherson, 1988, but can be distinguished by the following features:

- moveable finger of the cheliped bears a single basomesial spine
- P2–4 dactyli with about 10 ventral spines, the untimate at the base of the unguis.

Our specimens differ slightly from the illustrated lectotype material from Fiji and Ambon. The lectotype has the distomesial spine of antenna article 2 described as occasionally overreaching the end of the peduncle, while in both our specimens, the distomesial spine distinctly overreaches the distal end of the peduncle.

Distribution. Taiwan, Indonesia, Queensland, New Caledonia, Vanuatu, Wallis and Futuna, Fiji, T-onga, 190–1183 m. South-western Australia, 329–431 m.

Munida pectinata Machordom and Macpherson, 2005

Figure 20C

Munida pectinata Machordom and Macpherson, 2005: 828, fig. 3 (type locality: New Caledonia). — Baba, 2008: 112. — Komai, 2011: 359, fig. 10, 11D (colour) (Japan 96–221 m). — Komai, 2012: 38 (Izu islands, 174–192 m).

Material examined. Western Australia: NMV J55268, 4 males (2 damaged; cl 10.8 mm, pcl 6.5 mm; cl 18.4 mm, pcl 10.7 mm), 17° 35.706' S, 118° 58.902' E to 17° 35.346' S, 118° 58.794' E, 108–140 m, SS05/2007 stn 62, 16 June 2007.

Colour. Carapace and somites 2–4 pale orange with dark orange markings, somites 5–6 and telson pale orange. Rostrum and supraocular spines orange. Chela merus pink with red bands, remaining chela mottled orange. P2–4 white with orange/red bands.

Genetic data. COI and 16S; see Table 1.

Remarks. These Australian specimens of *M. pectinata* agree well with illustrations of type material from New Caledonia, extending the range to eastern Indian Ocean. The north-western Australian sequences of COI (639 bp) and 16S were identical to two sequences from New Caledonia. This is the first record of *M. pectinata* from Australia.

Distribution. New Caledonia, Japan and north-western Australia, 96–240 m.

Munida pherusa Macpherson and Baba, 1993

Munida pherusa Macpherson and Baba, 1993: 408, fig. 15 (type, locality: Philippines). — Baba et al., 2008: 112. — Baba et al., 2009: 178, figs 158–159. — Kim et al., 2016: 9, fig. 9 (Korea, 112–117 m).

Material examined. Western Australia: NMV J55097, 1 specimen, Ningaloo South, 22° 04.002' S, 113° 48.66' E to 22° 04.248' S, 113° 48.9' E, 101–106 m, SS10/2005/144, 10 December 2005; NMV J13307, 9 ovigerous females (cl 7.7 mm, pcl 4.5 mm to cl 11.4 mm, pcl 7.3 mm), 2 females (cl 8.3 mm, pcl 4.9 mm; cl 9.1 mm, pcl 7.3 mm), 7 males (cl 7.3 mm, pcl 4.9 mm to cl 12.7 mm, pcl 7.7 mm), North-west Shelf, between Port Hedland and Dampier, 18° 50' S, 117° 39' E to 18° 50' S, 117° 39' E, 178 m, NWA stn 29, 6 June 1983.

Remarks. In addition to one specimen of *M. pherusa* collected in 2005 in north-western Australia, another 17 specimens are reported here from a survey of the North-West Shelf in 1983. The specimens show that the length of the disto-mesial spine on antennal article 2 is slightly variable in length, sometimes just reaching the end of the peduncle and in some specimens, including the holotype, it slightly overreaches the peduncle. In the illustrated holotype, the cheliped finger is distinctly shorter that the palm, while in all of our specimens, the cheliped finger and palm are subequal in length.

These are the first records of *M. pherusa* from Australia.

Distribution. Japan, Philippines, Indonesia, Korea, 73–167 m. North-western Australia, 101–178 m.

Munida philippinensis Macpherson and Baba, 1993

Munida philippinensis Macpherson and Baba, 1993: 410, fig. 16 (type locality: Philippines). — Baba et al., 2008: 112.

Material examined. Western Australia: NMV J56003, 4 females (cl 7.9 mm, pcl 4.8 mm to cl 10.1 mm, pcl 9.0 mm), 12 males (cl 7.5 mm, pcl 4.8 mm to cl 11.2 mm, pcl 7.4 mm), Leveque L27, 14° 58.362' S, 121° 38.556' E to 14° 57.762' S, 121° 39.264' E, 228–232 m, SS05/2007/143, 2 July 2007.

Genetic data. COI and 16S; see Table 1.

Remarks. This is the first record of the species from Australia.

Distribution. Philippines, Indonesia, 146–297 m. North-west Australia, 228–222 m.

Munida pilorhyncha Miyake and Baba, 1966

Figure 21

Munida pilorhyncha Miyake and Baba, 1966: 81, figs 1, 2 (type locality: Tosa Bay, Japan). — Baba et al., 2008: 112 (synonomies, type data). — Baba et al., 2009: 180, figs 160–162 (Taiwan).

Munida sp. MoV 5200. — Poore et al., 2008: 20, unnumbered fig. (lower right). —McEnnulty et al., 2011: app. 1, 2.

Material examined. Western Australia: NMV J55145, 1 female (cl 21.5 mm, pcl 16.8 mm), Bunbury, 33° 00.504' S, 114° 34.26' E to 33° 00.12' S, 114° 34.5' E, 414–421 m, SS10/2005/13, 20 November 2005.

Colour. Carapace and somites 2–4 pale orange. Rostrum orange. Supraocular spines white. Cheliped with orange/red spots at base of spines and orange/red at distal ends of chela fingers.

Genetic data. Not available.

Remarks. Poore et al. (2008) and McEnnulty et al. (2011) reported the present specimens as "*Munida* sp. MoV 5200"; this is the first confirmed record of *Munida pilorhyncha* from Australia.

Distribution. Japan, South China Sea, Philippines, Taiwan, Kei Islands, Indonesia, 200–366 m. South-western Australia, 414–421 m.

Munida roshanei Tirmizi, 1966

Figure 20D

Munida roshanei Tirmizi, 1966: 192, fig. 13 (type locality: Gulf of Oman). — Baba, 2008: 116.

Material examined. Western Australia: NMV J55261, 1 male (cl 11.1 mm, pcl 7.2 mm), Barrow L1 transect, 21° 02.148' S, 114° 53.28' E to 21° 01.992' S, 114° 53.142' E, 90–100 m, SS05/2007/8, 10 June 2007; NMV J55991, 16 ovigerous females (cl 8.4 mm, pcl 5.0 mm to cl 10.9 mm, pcl 7.0 mm), 7 females (cl 8.5 mm, pcl 5.3 mm to cl 10.9 mm, pcl 6.7 mm), 22 males (cl 8.4 mm, pcl 4.9 mm to cl 11.2 mm, pcl 6.4 mm), Mermaid L24 transect, 17° 46.104' S, 120° 43.152' E to 17° 45.948' S, 120° 42.942' E, 97–109 m, SS05/2007/97, 20 June 2007; NMV J56400, 2 males (cl 8.9 mm, pcl 5.9 mm; cl 13.5 mm, pcl 8.0 mm), 2 ovigerous females (cl 9.9 mm, pcl 5.6 mm; cl 11.8 mm, pcl 6.8 mm), 3 females (1 damaged; cl 9.5 mm, pcl 5.6 mm to cl 10.0 mm, pcl 5.7 mm), 1 male (cl 8.9 mm, 5.9 mm), Broome L25 transect, 16° 45.156' S, 121° 02.796' E to 16° 44.592' S, 121° 02.208' E, 100–108 m, SS05/2007/116, 30 June 2007; NMV J56009, 2 ovigerous females (cl 10.9 mm, pcl 7.2 mm; cl 11 mm, pcl 7.8 mm), 1 male (cl 7.8 mm, pcl 4.7 mm), Lacepede L26 transect, 15° 48.672' S, 121° 03.738' E to 15° 48.426' S, 121° 03.654' E, 90–107 m, SS05/2007/125, 1 July 2007; NMV J56098, 4 males (cl 8.4 mm, pcl 5.1 mm to cl 11.7 mm, pcl 7.0 mm), 1 female (cl 10.6 mm, pcl 6.7 mm), Adele L28 transect, 14° 33.732' S, 122° 55.092' E to 14° 33.684' S, 122° 54.906' E, 95–105 m, SS05/2007/161, 4 July 2007; NMV J56395, 1 ovigerous female (cl 14.1 mm, pcl 8.6 mm), 1 female (cl 9.1 mm, pcl 5.2 mm), 3 males (cl 11.3 mm, pcl 6.9 mm to cl 11.8 mm, pcl 7.8 mm). Ashmore L30 transect, 12° 26.7' S, 123° 36.048' E to 12° 26.964' S, 123° 36.588' E, 95 m, SS05/2007/188, 6 July 2007; NMV J56007, 1 ovigerous female (cl 11.3 mm, pcl 7.2 mm), 1 female (cl 10.0 mm, pcl 6.3 mm), Ashmore L30 transect, 12° 25.944' S, 123° 35.784' E to 12° 26.064' S, 123° 35.868' E, 111 m, SS05/2007/196, 6 July 2007; NMV J55096, 1 male (missing chelipeds and rostrum; pcl 7.3 mm). Kalbarri, 27° 48.48' S, 113° 17.82' E to 27° 48.756' S, 113° 17.94' E, 112–123 m, SS10/2005/96, 4 December 2005; NMV J55047, 1 ovigerous female (missing chelipeds; cl 11.6, pcl 7.1 mm), 1 male (cl 12.8 mm, pcl 8.0 mm), 1 juvenile (cl 9.0 mm, pcl 5.4 mm), Barrow Island, 21° 01.896' S, 114° 53.52' E to 21° 02.064' S, 114° 53.28' E, 93 m, SS10/2005/169, 13 December 2005; NMV J55045, 1 female (cl 7.0 mm, pcl 5.0 mm), 6 males (cl 8.0 mm, pcl 4.3 mm to cl 12.7 mm, pcl 5.5 mm), Barrow Island, 20° 59.082' S, 114° 54.42' E to 20° 59.67' S, 114° 54.54' E, 100–101 m, SS10/2005/170, 13 December 2005; NMV J55048, 1 male (cl 10.2 mm, pcl 5.8 mm), SS10/2005/170.

Genetic data. COI and 16S; see Table 1.

Remarks. *Munida roshanei* is reported for the first time from Australia. Our specimens have much longer supraocular spines (0.36 times rostrum length) than figured for the type (0.2 times rostrum length) (Tirmizi, 1966: fig. 13). Longer supraocular spines are also present on the specimen from the Red Sea illustrated by Lewinsohn (1969). Our specimens all lack a row of median gastric spines behind the rostrum, whereas the type has a row of 3 median gastric spines behind the rostrum, and in other specimens 1 or 2 spines are reported (Baba, 1988; Tirmizi and Javed, 1993). There is clear sexual dimorphism in this species with males having large, gaping cheliped fingers. All of our specimens have cheliped fingers subequal to the palm in length.

Distribution. Indian Ocean (Gulf of Oman and Gulf of Aden, Red Sea, Andaman Sea and Mozambique Channel), and Phillipines, 16–528 m. Western Australia, 93–123 m.

Munida rubridigitalis Baba, 1994

Figure 22

Munida rubridigitalis Baba, 1994a: 13, fig. 6 (type locality: off Central Queensland). — Ahyong and Poore, 2004: 41. — Poore, 2004: 234 (compilation). — Baba, 2005: 273. — Baba et al., 2008: 117.

Not *Munida rubridigitalis* — Poore et al., 2008: 20 (south-western Australia, 396–411 m) (= *Munida julumunyju* sp. nov.).

? *Munida rubridigitalis*. — Macpherson, 1997: 610.

Munida sp. — Macpherson, 1994: 558, figs 13b, 90 (= *Munida julumunyju* sp. nov.).

? *Munida rubrodigitalis* [sic]. — Macpherson, 1999: 423, fig. 4e.

Type material. Paratypes: QM W19726, 2 males (pcl 10.0–12.7 mm), 3 ovigerous females (pcl 10.9–12.1 mm), 1 female (9.5 mm), Queensland, Coral Sea, 17° 51.13' S 147° 8' E, 497–503 m, Cidaris Station 47-2, 16 May 1986.

Other material examined. Queensland: AM P42278, 1 male (pcl 14.7 mm, cl 20.5 mm), 1 ovigerous female (pcl 16.6 mm, cl 23.0 mm), north-east of Tweed Heads, 27° 55–57' S, 154° 03' E, 549 m, trawl, K78-23-09, 6 November 1978.

New South Wales: AM P88982, 1 male (pcl 12.6 mm, cl 17.8 mm), 4 ovigerous females (pcl 12.4 mm, 17.3 mm to pcl 14.7 mm, cl 20.6 mm), north-east of Tweed Heads, 28° 01.8' S, 153° 58.8' E, 549 m, trawl, K78-09-05, 2 June 1978; AM P31504, 2 ovigerous females (pcl 13.1 mm, 18.9 mm; pcl 15.7 mm, cl 22.6 mm), south-east of Cape Byron, 28° 41–44' S, 153° 51' E, 156 m, K78-17-21, 5 April 1978; AM P31423, 1 female (pcl 16.0 mm, cl 22.5 mm), north-east of Sugarloaf Point, 32° 15' S, 153° 02' E, 457 m, trawl, K78-03-04, 5 April 1978; AM P31502, 1 male (pcl 13.4 mm, cl 19.5 mm), 1 female (pcl 13.1 mm, cl 18.4 mm), north-east of North Solitary Island, 29° 53–50' S, 153° 42–43' E, 457 m, trawl, K78-06-07, 24 April 1978; AM P66658, 2 females (pcl 10.4 mm, cl 14.9 mm; pcl 12.2 mm, cl 18.0 mm), north-east of Long Reef, 33° 42' S, 151° 42' E, K85-21-06, 439–466 m, K85-21-06, 19 December 1985.

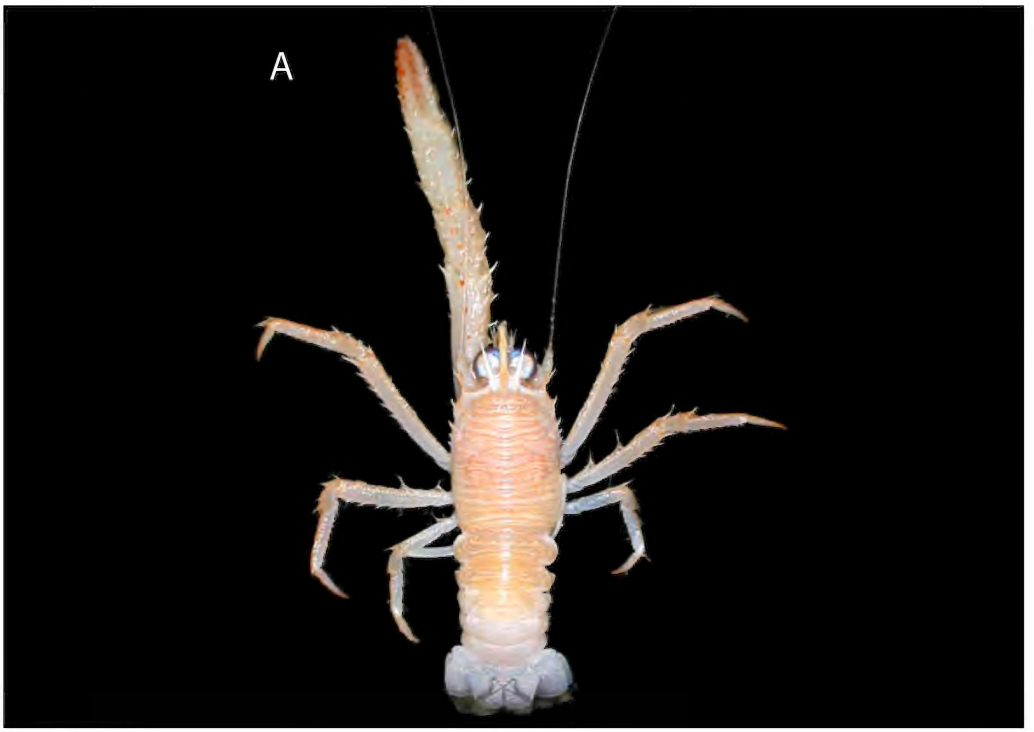


Figure 21. *Munida pilorhyncha* Miyake and Baba, 1966, female, cl 21.5 mm pcl 16.8 mm, (NMV J551451).

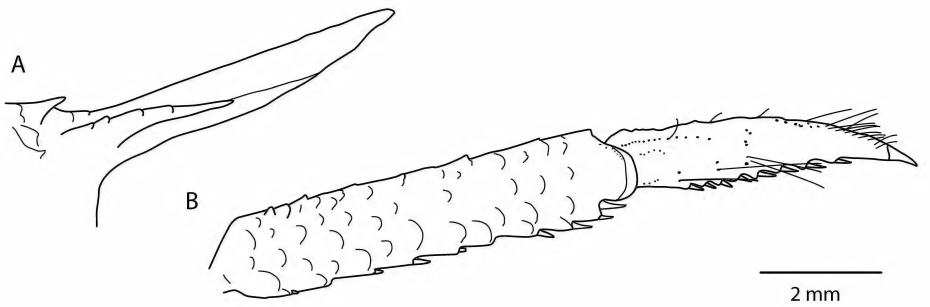


Figure 22. *Munida rubridigitalis* Baba, 1994. Baba, 1994, paratype, male cl 16.2 mm, pcl 10.2 mm (QM W19727): A, rostrum; B, right P2 dactylus and propodus. Scale: A–B = 2 mm

Genetic data. Not available

Remarks. *Munida rubridigitalis*, described from Queensland, has been also reported from New South Wales, north-western Australia, New Caledonia, Vanuatu, Indonesia (Kei islands) (Macpherson, 1994, 1997, 1999; Ahyong and Poore, 2004; Baba et al., 2008; Poore et al., 2008). The north-western Australian records of *M. rubridigitalis* are herein shown to be referable to a separate species, *M. julumunyju* sp. nov., which differs chiefly in having a deeper, more strongly curved rostrum (see account of that species). We compared paratypes and other Australian material of *M. rubridigitalis* to six MNHN specimens identified as *M. rubridigitalis* from New Caledonia (see material listed under *M. julumunyju*). These New Caledonian specimens are herein referred to *M. julumunyju* sp. nov., as are specimens reported from New Caledonia and the Loyalty Islands as *Munida* sp. by Macpherson (1994). Thus, other records of *M. rubridigitalis* from New Caledonia, Kei Islands and Vanuatu could also be referable to *M. julumunyju* sp. nov. (see *Remarks* for that species). At present, *M. rubridigitalis* sensu stricto is known only from eastern Australia.

Distribution. Eastern Australia, from Queensland and New South Wales, 156–549 m.

Munida sacksi Macpherson, 1993

Munida sacksi Macpherson, 1993: 438 (part), fig. 6 (type locality: Philippines). — Baba et al., 2008: 119.

Munida sp. MoV 5217. — Poore et al., 2008: 21. —McEnnulty et al., 2011: app. 1.

Material examined. Western Australia: NMV J55039, 1 male (cl 11.6 mm, pcl 8.2 mm), Ningaloo South, 22° 04.314' S, 113° 45.36' E to 22° 04.854' S, 113° 45.36' E, 387–399 m, SS10/2005/151, 10 December 2005.

Genetic data. Not available.

Remarks. *Munida sacksi* was described from the Philippines, based on a single female, missing the chelipeds. The present specimen, reported by Poore et al. (2008) as "*Munida* sp. MoV 5217", represents the first record of the species from Australia.

Distribution. Philippines, 300–330 m. Western Australia, 387–399 m.

Munida shaula Macpherson and de Saint Laurent, 2002

Munida shaula Macpherson and de Saint Laurent, 2002: 474, figs 3A–C, E–H [type locality: Réunion Island]. — Baba et al., 2008: 117.

Munida sp. MoV 5215. — Poore et al., 2008: 21. — McEnnulty et al., 2011: app. 1.

Material examined. Western Australia: NMV J55111, 1 ovigerous female (cl 15.3 mm, pcl 9.9 mm), Ningaloo North, 21° 58.212' S, 113° 47.58' E to 21° 58.752' S, 113° 47.46' E, 324–356 m, SS10/2005/157, 11 December 2005.

Genetic data. Not available.

Remarks. This specimen, reported as "*Munida* sp. MoV 5215" by Poore et al. (2008), agrees well with *Munida shaula*, previously recorded from the western Indian Ocean (Reunion Island, Madagascar and Zanzibar). This is the first confirmed record of *M. shaula* from Australia.

Distribution. Zanzibar, Madagascar, La Réunion and Mozambique, 263–510 m. Western Australia, 324–356 m.

Munida typhle Macpherson, 1994

Munida magniantennulata. — Baba, 1994: 12.

Munida typhle Macpherson, 1994: 549, fig. 60 (type locality: New Caledonia). — Baba et al., 2008: 126. — Baba et al., 2009: 200, figs 181–182. — Poore et al., 2011: pl. 18H (colour). — Macpherson, 2013: 306. — Macpherson et al., 2017: 54.

Munida cf. *magniantennulata*. — Farrelly and Ahyong, 2019: 13, 55, fig. 98.

Material examined. Queensland: QM W19722, 1 female (cl 12 mm, pcl 7.5 mm), Coral Sea, 17° 45.04' S, 147° 48.014' E, 1223–1228 m, CIDARIS I stn 20-4, 10 May 1986; QM W19721, 1 female (cl 7.5 mm, pcl 5.0 mm), Coral Sea, 16° 50.133' S, 147° 10.1' E, 1607–1609 m, CIDARIS I stn 35-3, 14 May 1986; NMV J72915, 1 ovigerous female cl 21.9 mm, pcl 13.8 mm, Coral Sea CMR, 23° 37.872' S, 154° 39.582' E to 23° 39.54' S, 154° 38.628' E, 1761–1770 m, IN2017_v03 stn 128, 13 June 2017.

Genetic data. Not available

Remarks. The present specimens referred to *M. typhle* were recorded by Baba (1994) from central Queensland as *M. magniantennulata*. These two species are very similar overall, but the cheliped of *M. typhle* has spines present on the dorsal face of the palm and 2 lateral spines on the proximal half of the fixed finger, which are absent in *M. magniantennulata*. In addition, the P2–4 dactyli are longer in *M. typhle* (0.8 times the propodus compared to 0.5–0.6 in *M. magniantennulata*); and abdominal somite 2 has 4 spines on the anterior ridge while *M. magniantennulata* has 2 spines. In the Queensland specimens examined here, the P2 dactylus has 7–8 spines along the flexor margin compared to the holotype of *M. typhle,* with 9 spines. The QM registration numbers published by Baba (1994) were listed incorrectly and have been corrected here. The ovigerous female (NMV J72915; Ahyong and Farrelly, 2019: fig. 98) collected during the recent Investigator voyage is much larger than most specimens collected previously. This large female differs from other specimens in lacking spines on the cheliped dactylus, and the spines on abdominal somite 2 are proportionally longer (similar in length to the branchial margin spines) and limited to the median part of the anterior ridge.

Distribution. Somalia coast, Seychelles, southern Madagascar, Taiwan, New Caledonia, Vanuatu, French Polynesia, 500–1940 m. Queensland, 1607–1761 m.

Acknowledgments

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Phylogenetic placement of a recently discovered population of the threatened alpine she-oak skink *Cyclodomorphus praealtus* (Squamata: Scincidae) in Victoria

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Abstract

Sumner, J., Haines, M.L., Lawrence, P., Lawrence, J. and Clemann, N. 2021. Phylogenetic placement of a recently discovered population of the threatened alpine she-oak skink *Cyclodomorphus praealtus* (Squamata: Scincidae) in Victoria. *Memoirs of Museum Victoria* 80: 153–157.

The alpine she-oak skink *Cyclodomorphus praealtus* is a threatened alpine endemic lizard from the mainland of Australia. The species is previously known from disjunct populations in Kosciuszko National Park in New South Wales and three isolated localities in the Victorian Alps. The New South Wales and Victorian populations represent separate evolutionarily significant units. In 2011, a fourth Victorian population was discovered. We conducted a phylogenetic analysis and determined that the newly discovered population is discrete and may have been separated from other populations since the end of the last glacial maxima. This population requires separate management.

Keywords

Cyclodomorphus praealtus, phylogenetic relationship, conservation, threatened species

Introduction

The alpine she-oak skink *Cyclodomorphus praealtus* Shea (1995) is restricted to sky island plains (*sensu* Koumoundouros et al., 2009) above 1500 m elevation in the mainland Australian alpine bioregion (Cogger, 2014). The species has been recorded in New South Wales (NSW) at Kosciuszko National Park and in Victoria at the Bogong High Plains, around Mt Hotham, Mt Higginbotham and Mt Loch, and on the Dargo High Plains at Lankey and Omeo Plains (Clemann, 2011; fig. 1). The Victorian sites are all within approximately 30 km of each other (Table 1). The species has specific habitat requirements, occurring in alpine heathland and alpine grassy heathland. These habitats generally have a disjunct occurrence and are within a matrix of other alpine and sub-alpine habitats in which the alpine she-oak skink is not known to occur. Within some locations, the species distribution is further fragmented by ski resort buildings and groomed ski slopes, roads and tracks. The species is listed as nationally endangered under the federal *Environment Protection & Biodiversity Conservation Act 1999*, threatened in Victoria under that state's *Flora and Fauna Guarantee Act 1988*, critically endangered in Victoria by the Department of Sustainability and Environment (2013) and endangered in NSW under the *Threatened Species Conservation Act 1995*. The species is considered at risk from climate change (Clemann, 2003; Koumoundouros et al., 2009) and is a high priority for conservation management.

Populations of *C. praealtus* in NSW and Victoria are reciprocally monophyletic at the mtDNA ND4 loci, with a 4.28% net sequence divergence between regions, and it was recommended that they be treated as separate evolutionarily significant units (Koumoundouros et al., 2009). The three known Victorian populations exhibit strong genetic structure, with no current inter-population gene flow, despite evidence for historical connectivity (Koumoundouros et al., 2009). This concurs with their present disjunct distribution on high elevation plateaux and peaks in alpine meadows that are separated by valleys of eucalypt forests.

In 2011, *C. praealtus* was discovered at a fourth Victorian locality – the Wellington Plains (Clemann et al., 2016). This is the southern-most area where this species has been recorded and is 58 km from the closest Victorian population at Lankey Plain. Here we present a phylogenetic analysis to determine the relationship between this new population and those studied by Koumoundouros et al. (2009). Our results provide information that will assist the conservation management of this species.

Table 1. Divergence among five populations of *Cyclodomorphus praealtus* in Victoria (VIC) and New South Wales (NSW). Uncorrected p-distance (number of base substitutions per site averaged over all sequence pairs between groups; bottom) and straight-line distance (km) between locations (top).

	Bogong High Plains, VIC	Mt Hotham, VIC	Lankey Plain, VIC	Wellington Plains, VIC	Mt Kosciuszko, NSW
Bogong High Plains, VIC	–	31	29	96	101
Mt Hotham, VIC	0.01	–	34	71	117
Lankey Plain, VIC	0.012	0.009	–	58	126
Wellington Plains, VIC	0.016	0.019	0.018	–	193
Mt Kosciuszko, NSW	0.052	0.052	0.055	0.059	–

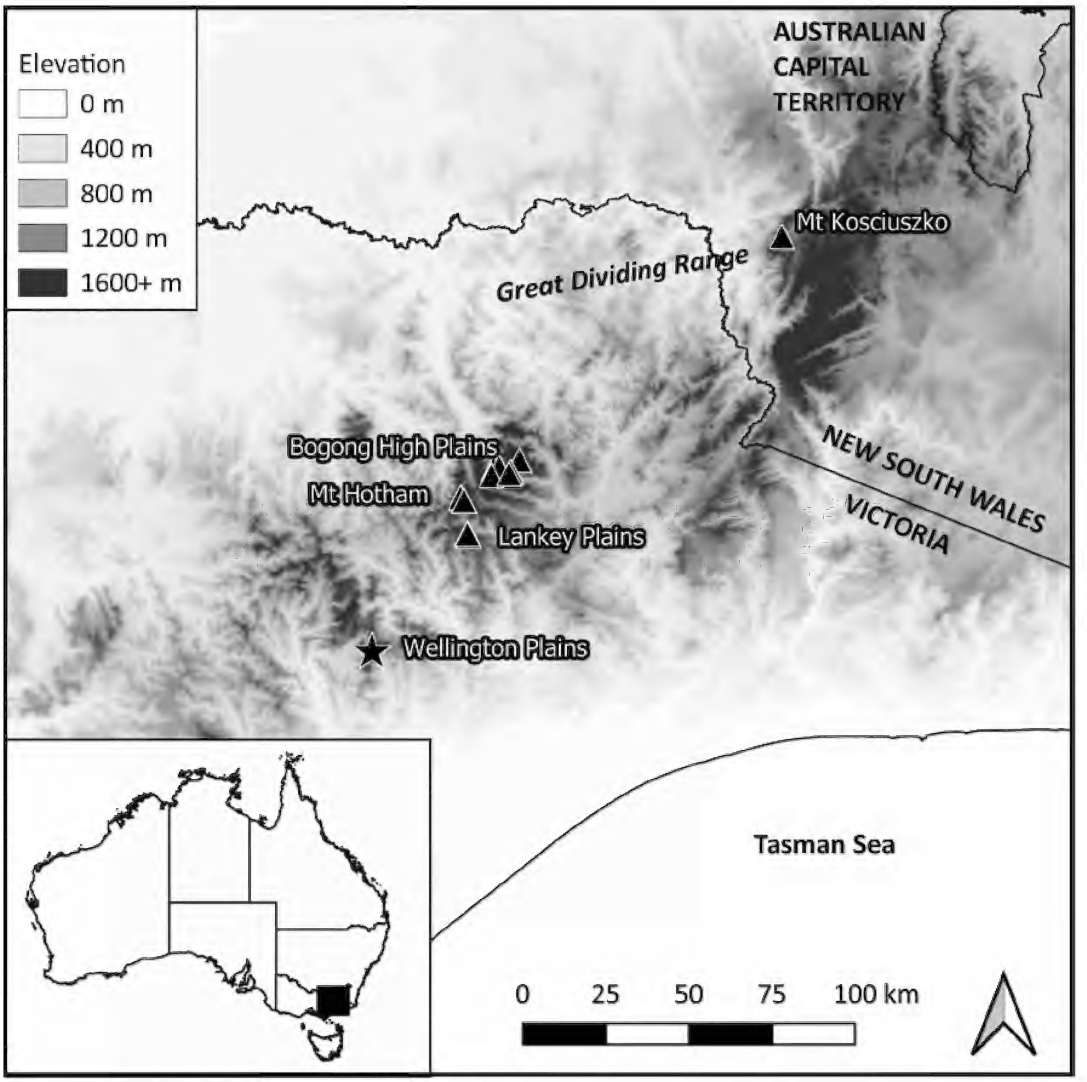

Figure 1: Elevation map of the mainland Australian alpine region indicating the five major populations of *Cyclodomorphus praealtus*, including the new location of Wellington Plains. Elevation is indicated by light, mid and dark grey areas at 500 m intervals, with highest elevations at or above 1500 m above sea level. Adapted from fig. 1; Koumoundouros et al. (2009).

Methods

Discovery of this population of *C. praealtus* and collection of tissue samples is described by Clemann et al. (2016). Tissue samples (tail tips) were collected from two sub-adult *C. praealtus* from the Wellington Plains (1530 m elevation; fig. 1) in November 2011.

We extracted genomic DNA using a Qiagen DNeasy® Blood and Tissue Kit according to the manufacturer's instructions (www.qiagen.com). An 850 base pair region of the mtDNA NADH dehydrogenase subunit 4 (ND4) gene was chosen for sequencing because it has useful levels of variability in this species and in related skink groups (Chapple and Keogh, 2004; Koumoundourus et al., 2009). ND4 was amplified according to the protocols and conditions in Koumoundouros et al. (2009) using the primer pair ND4I (5' TGACTACCAAAAGCTCATGTAGAAGC 3'), and tRNA-leu (5' TACTTTTACTTGGATTTGCACCA 3'; Chapple and Keogh, 2004). The resulting polymerase chain reaction product was purified using ExoSAP-IT® (Affymetrix), and the purified products were sent to Macrogen (South Korea) for sequencing.

Forward and reverse sequences were assembled in Geneious R6.1.8 (Biomatters Ltd.) and were aligned against 103 published sequences and outgroups for this species (Koumoundouros et al., 2009) using default settings in ClustalW. We translated the protein-coding regions into amino acids and did not observe stop codons or indels. IUPAC ambiguity codes were used for heterozygous sites. We trimmed the alignments to 758 base pairs because the end of the sequences could not be aligned due to the length-variable loops and stems of the tRNA genes. The Wellington Plains sequences were deposited in GenBank.

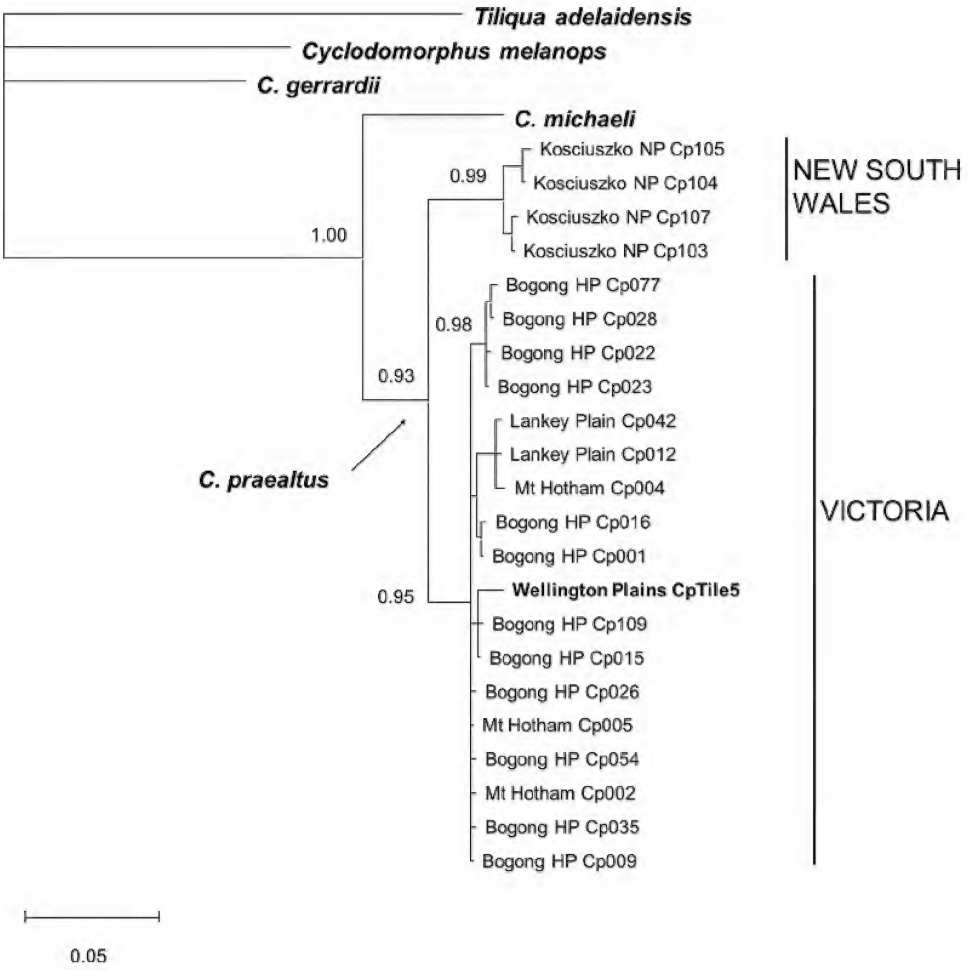

Figure 2: A Bayesian consensus tree of the mtDNA ND4 sequences, depicting the relationship between unique haplotypes at each locality (Bogong High Plains, Lankey Plain, Mt Hotham, Wellington Plains and Kosciuszko National Park) for *Cyclodomorphus praealtus*. Bayesian posterior probabilities are shown at major nodes.

To determine the relationship of the Wellington Plains population to all other known populations, we created a phylogenetic tree. Only unique haplotypes were used. We used Modeltest 3.7 (Felsenstein, 1985) with the PAUP* plug-in run within Geneious R6.1.8 to determine which of the 56 potential models of DNA sequence evolution was most suitable for our data. The GTR+G model of evolution was selected as the most appropriate model using the Akaike information criterion (Akaike, 1974). The MrBayes version 3.2.6 (Huelsenbeck et al., 2001; Ronquist and Huelsenbeck, 2003) plug-in within Geneious R6.1.8 was used to conduct a Bayesian Markov chain Monte Carlo phylogenetic analysis using two million generations sampled every 500 generations, with four heated chains sampling independently and a 25% burn-in. Chain convergence was confirmed by examining the log trace in Geneious and estimated sample size values > 200. The mean between group distance was calculated among all five populations in MEGA6 (Tamura et al., 2006).

To infer the relationship between the mitochondrial ND4 sequences from Wellington Plains and the published haplotypes in Victoria, we created a statistical parsimony network using the program TCS (Clement et al., 2000) using a 95% statistical confidence limit for the maximum number of nucleotide substitutions between two haplotypes.

Results

The ND4 sequences comprised 758 base pairs, including 63 variable sites and 50 parsimony informative sites. The sequences from the two Wellington Plains individuals were identical and differed from all previously known haplotypes. The Bayesian consensus tree (fig. 2) revealed that the ND4 haplotype from Wellington Plains falls within the monophyletic Victorian lineage and did not group with any other populations. The Wellington Plains haplotype differed from the populations in Victoria by 1.6–1.9% and from the NSW population by 5.9% (Table 1).

A haplotype parsimony network of all ND4 sequences generated in TCS (fig. 3) indicates that the Wellington Plains haplotype forms a third distinct haplogroup cluster, separate from all other Victorian haplotypes, and that they cluster more closely with the north-eastern haplogroup that includes individuals from Bogong High Plains and Mt Hotham. Eight nucleotide changes separate the Wellington Plains sample from the closest haplotype from the Bogong High Plains.

Discussion

Analysis of mtDNA ND4 sequences of two *C. praealtus* individuals from Wellington Plains indicates the presence of a haplotype that is not found in any other population across the restricted range of this alpine endemic species. Further work using multiple nuclear genes is needed before we can confirm that the Wellington Plains population is isolated from the other Victorian populations as the current data suggests. It is not possible to determine the level of genetic diversity within the Wellington Plains population due to the small sample size.

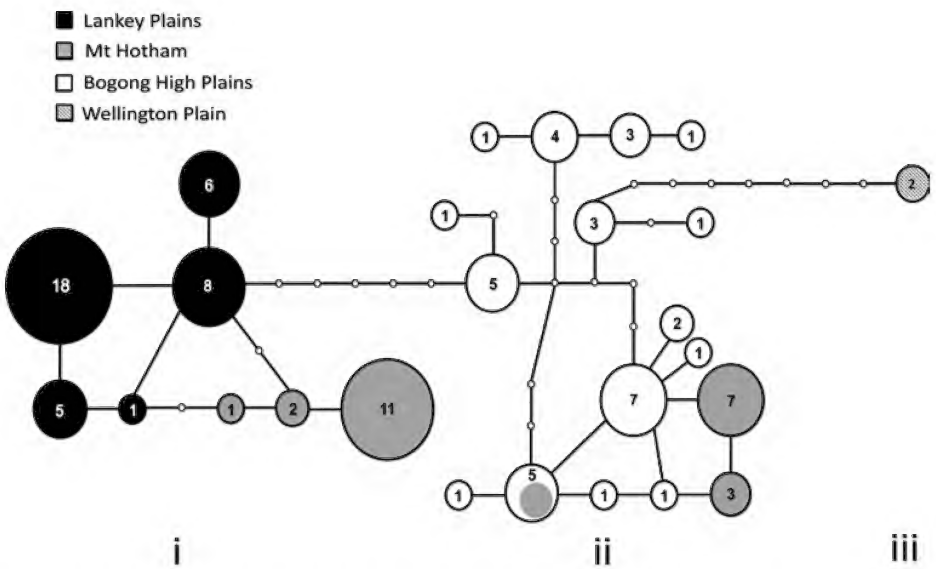

Figure 3: Population structure of Victorian *Cyclodomorphus praealtus* according to ND4 mitochondrial haplotype network. Black indicates individuals from Lankey Plain, dark grey indicates those from Mt Hotham, white indicates those from Bogong High Plains and diagonal stripes indicate those from Wellington Plains. The network structure indicates 3 haplogroups (i, ii and iii) within Victoria. Each circle represents a unique haplotype, with the circle size indicative of frequency and sample sizes within each circle. Empty circles represent missing haplotypes and differ by one base pair from the closest haplotype.

The Wellington Plains population is the most divergent of the populations in Victoria, with 1.6–1.9% sequence divergence from the other populations, compared with the 0.9–1.2% divergence among the other Victorian populations. Using the conventional vertebrate mtDNA clock calibration of 2% sequence divergence per million years (Avise, 2004), suggests a divergence time between Wellington Plains and the other populations in Victoria of between 500 000 and one million years before present. This places the divergence during the late Pliocene to early Pleistocene, during which climatic oscillations intensified resulting in rapid fluctuation between cool-dry and warm-wet conditions across south-eastern Australia (Markgraf et al., 1995). However, this predates the most recent glacial period from approximately 25 000–18 000 years before present, during which the alpine habitat extended into the valleys connecting the mountain peaks, allowing gene flow between populations of other alpine endemics.

In 2019 severe bushfires burned across the entire Wellington Plains plateau and, as a result, the status of this population is now uncertain. Surveys to determine whether the population still remains on the Wellington Plains are an urgent priority, both to confirm the status of this population and to identify any other specific threats. Threats already identified for *C. praealtus* in the Victorian Alps include climate change, loss and degradation of habitat (due to a range of processes, including several severe fires in the last decade, construction and maintenance of infrastructure and roads, grazing and trampling by exotic herbivores, and recreational activities), and predation by exotic carnivores (Clemann, 2003, 2013). Historically, loss and degradation of the habitat of *C. praealtus* due to cattle grazing also occurred in the Alpine National Park, and damage from this impact remains evident in parts of this lizard's range in Victoria (N. Clemann pers. obs.). Other reptiles endemic to the mainland alpine region also occur on the Wellington Plains, including threatened species such as the alpine bog skink *Pseudemoia cryodroma* and the tussock skink *P. pagenstecheri*. The fact that this population of *C. praealtus* remained unknown until so recently demonstrates that further surveys of Victorian alpine environments are needed if we are to document and effectively manage the biodiversity of this region, especially in the face of increasingly frequent and devastating bushfires.

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The unusual genus *Ramiheithrus* (Trichoptera: Philorheithridae)

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Abstract

St Clair, R.M.. 2021. The unusual genus *Ramiheithrus* (Trichoptera: Philorheithridae). *Memoirs of Museum Victoria* 80: 159–168.

The descriptions of males of the two described species of *Ramiheithrus* (*R. virgatus* Neboiss and *R. kocinus* Neboiss) are expanded using additional material. The female, pupa and larva of *Ramiheithrus virgatus* are described for the first time for the genus. Preliminary genetic barcoding analysis suggests the presence of additional undescribed species that are only known as larvae. The unusual larval habitat is described and issues relating to this are discussed.

Keywords

Australia, groundwater habitat, COI gene, pectinate antennae

Introduction

The genus *Ramiheithrus* was created for two species, one each in Victoria and Tasmania, by Neboiss (1974) with only adult males known at the time. Information here brings the number of species in the genus to four but the two additional species are known only as larvae. The descriptions of males of the two described species are revised here, partly based on specimens from additional sites. Figures indicating differences from the original descriptions, or those showing additional information, are included for males. The adult female, pupa and larva of *Ramiheithrus virgatus* Neboiss are described. The larva of *R. virgatus* is compared with the larvae of two additional species.

The "rami" in *Ramiheithrus* refers to the distinctive pectinate antennae. Pectinate antennae are otherwise unknown in Trichoptera, except for three species of the Odontoceridae genus *Phraepsyche* from South East Asia (Oláh and Johanson, 2010) although the form of the pectination is apparently different. A fossil trichopteran with yet another form of pectination is discussed in Gao et al. (2016).

Few females of Philorheithridae are described and there is variation between species in genera where more than one species is known. *Philorheithrus* now has females of four species described, and these show considerable variation in shape of genitalia (Henderson and Ward, 2006; Mosely and Kimmins, 1954). This suggests that females of other *Ramiheithrus* species may differ from the description below. The vaginal apparatus of *R. virgatus* is illustrated below but there is no information on other Philorheithridae females to compare with.

Larvae of *Ramiheithrus* have very rarely been collected. The few available specimens provide information on variation in the larvae and the likely reason for this rarity.

DNA barcoding data is preliminary but has assisted taxonomic decisions.

Material and methods

The terminology here follows Henderson and Ward (2006) and Holzenthal et al. (2007) but not Neboiss (1974).

All specimens are lodged in the Museum of Victoria (NMV) and have been assigned registration (TRI) numbers. Reared specimens usually include the case with pupal closure membranes and larval sclerites, pupal skin and adult. The adult has not emerged from the pupal skin in some cases and wing venation cannot be discerned. Tissue samples sent to the Barcode of Life Data System (BOLD; http://www.boldsystems.org) for sequencing and analysis have been allocated LTUT numbers. Information on the methods used for sequencing and gene segment sequenced are available on the BOLD website. Data for specimens included in fig. 24 and Table 1 are available from the BOLD website. The neighbour joining tree (fig. 24) was produced on the BOLD website using a Kimura 2 parameter and BOLD aligner (amino acid–based HMM) and produced in Newick format using MEGA 7 on 26 October 2019.

Taxonomy

Ramiheithrus Neboiss

Type species: *Ramiheithrus virgatus* Neboiss

The information here uses and extends that given by Neboiss (1974).

Diagnosis. This genus is strikingly unique with the antennae of the adult pectinate on the basal half (fig. 1). In males, the superior appendages are fused to segment IX and in basal half to each other to form a hood over the genitalia (figs 2, 3, 22). This is like the hood in *Kosreithrus* and, to a lesser extent, some species of *Aphilorheithrus*. In *Ramiheithrus*, the superior appendages have

the ventral surfaces covered with moderately long spines in the distal third. The inferior appendages are short and very simple, most similar to those of *Kosrheithrus*. As with most Philorheithridae, the forewing has vein R1 joining R2 just before the wing margin in both sexes. However, this join is not present in some specimens in some populations of *R. virgatus* (fig. 5) and *R. kocinus* (fig. 23) and seems to be absent in at least some species in other genera. The forewing has 0 to 5 crossveins present between Sc and the costa proximal to the level of the r vein in both species, fewer than most *Aphilorheithrus* species but otherwise unusual in the family (fig. 5). The hind wing of both sexes with Sc and R1 merged for a short distance before separating and diverging again (fig. 5). Spiracles on pleura ventrally on segments 2 to 4 enlarged, elongate and variably fleshy, smaller and more rounded on segments 5 to 8, only lightly sclerotised around them (fig. 4).

In the larva, the anterior part of the frontoclypeal apotome is almost twice as wide as posterior to the constriction (figs 10, 24, 26). On the mid leg, the strong dark distal spine on the tibia remains despite the segment being fused with the tarsus (fig. 14). This spine is not present in other Australian Philorheithridae genera, although long and short pale setae are often present in this region. The larval case has the posterior opening almost completely closed by larger sand grains and large flat mineral particles but with gaps between these particles (fig. 17).

Generic diagnoses are not given for females or pupae because they are known from one species only.

Description. Head: pilifers absent; maxillary palps 5-segmented, long and slender in both sexes; labial palps short, about as long as maxillary palps segments one and two combined; antennae about as long as forewing, first segment stout, slightly longer than vertical diameter of eye, second segment very short, next 14 to 16 segments with long lateral branches, becoming shorter on the more distal segments, first 2 or 3 segments may have branched rami (fig. 1); a pair of small anterior setal warts near midline, pair of large, elongate, kidney-shaped posterior setal warts and pair of posterolateral setal warts encircling posterior half of eye. Thorax: 2 pairs of warts on pronotum, most medial pair elevated; 1 pair of rounded scutal warts, usually larger than scutellar warts; male forewing length 9 to 12 mm and lobe on anal margin strongly sclerotised, apex broad apically truncate, forks 1, 2, 3 and 5 present, male hind wing with forks 1, 2, 3 and 5, fork 3 footstalk of variable length. Abdomen: a small projection on sternite VII, variable in size.

Male genitalia: superior appendages moderately long, deeply excised, very broad and fused basally to segment IX and each other forming a hood, ventral surface of each with short pointed spines covering apical half; segment X (trilobed hood–like plate of Neboiss, 1974) trilobed, lateral lobes similar to each other but different to median lobe; inferior appendages a simple short broad plate, sometimes scooped out apically, almost bilobed in some specimens (figs 2, 3, 22). Phallus narrow, tapering apically.

Larva. Final instar about 9 to 12 mm long. Head: rounded and somewhat flattened dorsally; strong carinae present just above the eye from the anterior margin to about three quarters head length, forming the lateral margin of the head on each side; region between the carinae sloping ventrally near each carina which are raised above the head surface, roughened by minute protuberances; antennae very short, close to front of head and below carinae; labrum with 3 pairs of setae at about 3/4 length and another 3 pairs of short stout setae on front margin, lateral two pairs curved along margin; ventral apotome about 1/15 length of ventral ecdysial line; head setation as in fig. 10, most setae on the dorsal surface (but not on the carina) are short and very pale usually bent over or lying flat. Thorax: metanotum with 3 pairs of sclerites, anteriomedial pair about 4 times as long as posterior pair (figs 11, 24); prosternum with a large posterior central sclerite (figs 12, 25); mesosternum with 2 pairs of closely aligned sclerites medially, smaller and paler than pronotal sclerite, posterior pair rectangular, anterior pair tapering laterally (fig. 12); forelegs each with cluster of more than 12 stout black setae centrally on anterior face of femur, all arising from same point (fig. 13), tibial spur about 1/3 tarsal length, tarsal claw about half as long as tarsus, apical spine of tarsal claw almost as long as tarsal claw and lying closely along its length; mid leg tarsal claw about 1/5 tibiatarsus, basal spine of claw almost as long as tarsal claw and lying closely along its length; hind legs much longer than forelegs, tarsal claw about half tarsal length, 2 tibial spines on each tibiae about 1/3 tarsal length, 1 on anterior face, 1 ventral, a group of short spines apicoventrally (fig. 14). Abdomen: tergite IX short, not completely covering the segment, lightly sclerotised, with fringe of about 14 long setae and about 30 short or moderate length setae (fig. 15). The lightly sclerotised channel running ventrally from the base of anal claw towards the ventral junction of the prolegs is deeper and more obvious than in some other genera (fig. 16). This channel is darkly sclerotised at the deepest point near the base of the anal claw. Anal claws with tooth almost 1/2 length of claw.

Ramiheithrus virgatus Neboiss, 1974:

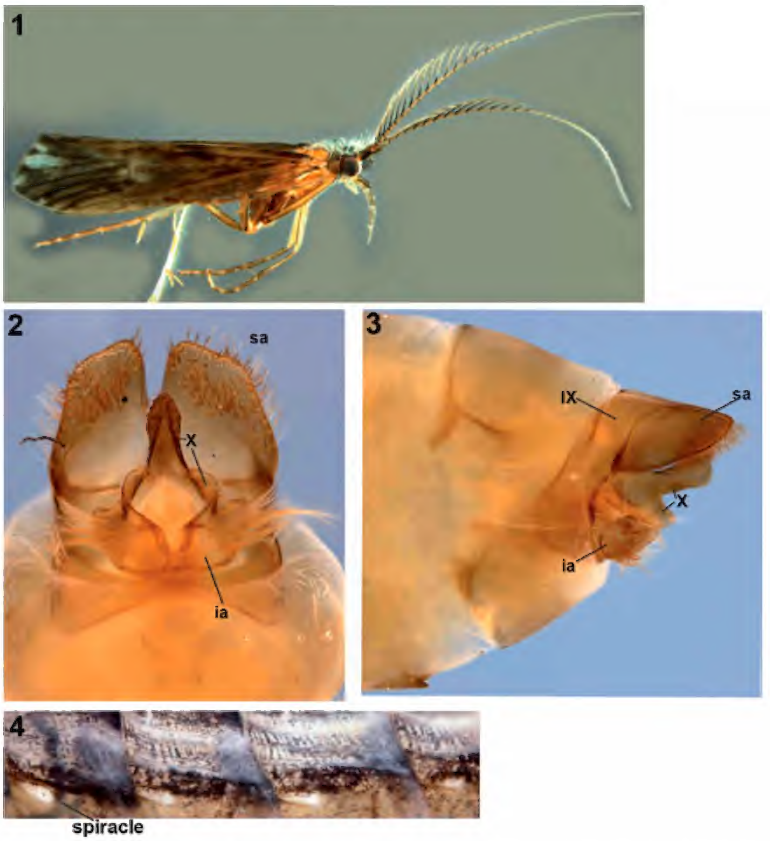
Figures 1–21

Type Material. Holotype male, Victoria. McKay Creek, Sassafras Gap, 36° 36' S 147° 47' E, 2 February 1974, A. Neboiss (NMV TRI-4558). Paratypes 8 males, collected with holotype (NMV TRI-4559 to 4566).

Other Material examined. New South Wales. Alpine Creek Kiandra, 35° 52' S 148° 29' E, 20 January 1966, 3 males 2 females (NMV TRI-29289), 16 January 1968, 1 male (NMV TRI-29288), 13 December 1974, 2 males, 3 females (NMV TRI-29290), E.F. Riek. Victoria. Roadside trickles 1.2 km N of Sassafras Gap, –36.6° E 147.79° S, 10 February 2010, 1 larva (LTUT720-12) (NMV TRI-54703), D. Cartwright and R. St Clair, 19 December 2013, 1 larva (NMV TRI-55169), D. Cartwright; Roadside seep 1.6 km N of Sassafras Gap, 10 February 2010, 1 larva (NMV TRI-55167), 11 February 2010, preserved assorted dates to 21 February 2010, 3 reared males, 1 reared female, 2 male pupae, 1 female pupa all with larval case and sclerites, 6 larvae (NMV TRI-54806 to 54815), D. Cartwright and R. St Clair; Whites Bridge Mt. Buller Road 5 km SE Mirimbah, 37° 08' S 146° 26' E, 22 Mar 1985, 1 male A. Neboiss (NMV TRI-29291), 1 male, 2 Jan 2011, M. Shackleton (LTUT723-12) (NMV TRI-54702).

Diagnosis. As for the generic diagnosis with the following additions. Male genitalia with segment X median lobe elongate, longer than lateral lobes (figs 2, 3).

Larva distinguishable from larvae of the two other species in the genus by the absence of small anterior sclerites on the



Figures 1–4. *Ramiheithrus virgatus* male: 1, Sassafras Gap body lateral; 2, Mt Buller genitalia ventral; 3, Kiandra genitalia lateral; 4, Mt Buller abdomen lateral showing elongate spiracles on segments. ia = inferior appendage, sa = superior appendage, IX = segment IX, X = segment X.

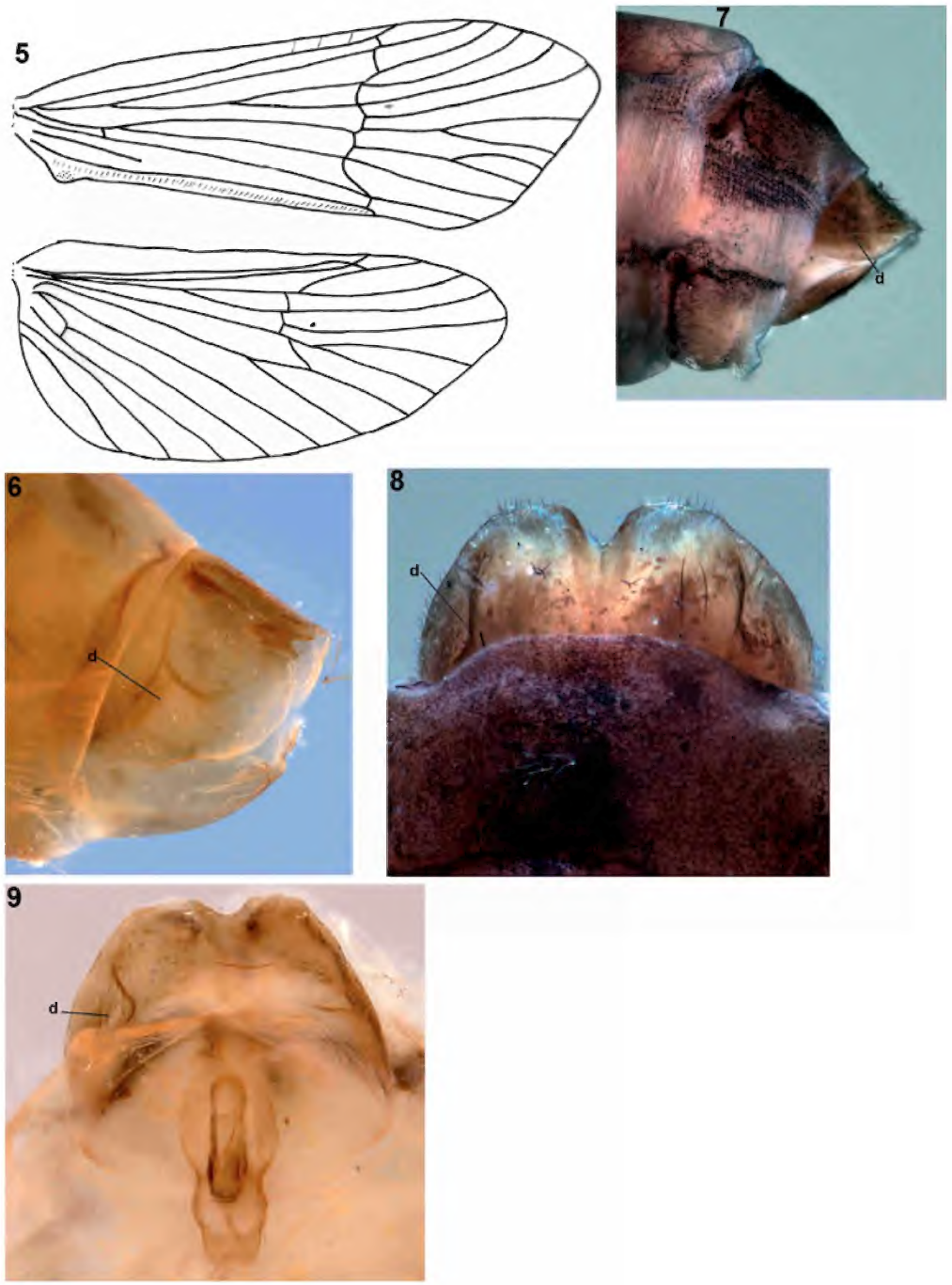
prosternum, the more strongly developed brush of small spines apically on the hind legs (fig. 14) and the reddish-brown head and thorax (fig. 11). Collection of additional larval specimens of the two undescribed species may show these larval characters to not be as diagnostic.

Description. Revised after Neboiss (1974). As for the generic description with the following. Antennae rami dark brown, antennal segments yellowish. Forewings irregularly mottled greyish brown, a distinct pale oval spot close to wing margin within fork 3, smaller and less conspicuous ones between the veins above and below it (fig. 1); R1 joins R2 in males and females although R1 joins the wing margin instead in most specimens collected near Kiandra (fig. 5) and a few from Sassafras Gap.

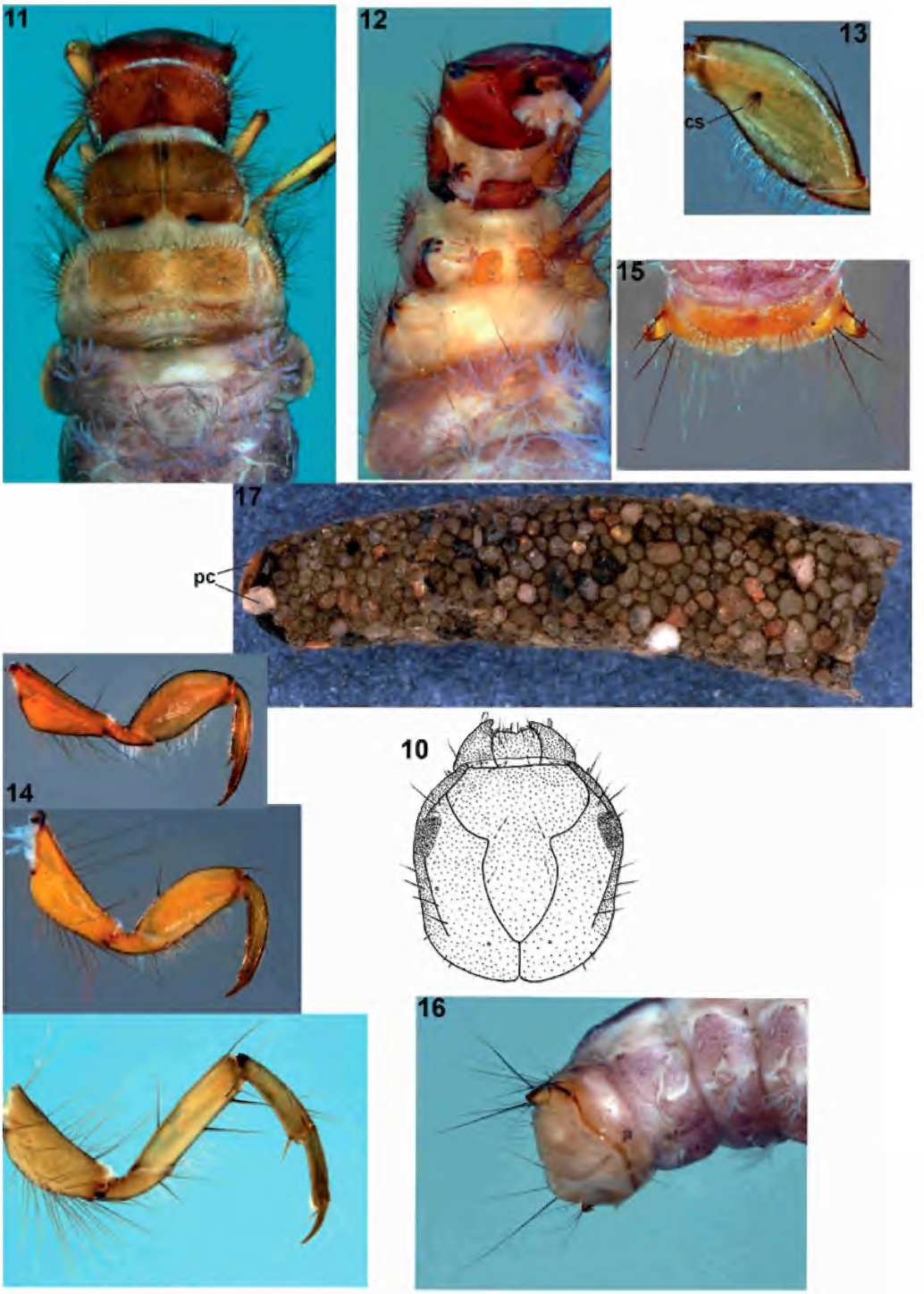
Male genitalia: segment X median lobe laterally compressed, lobe longer than lateral lobes; lateral lobes flat, somewhat truncate in lateral view; phallus comes to a point apically, curved downwards ventrally; inferior appendages somewhat truncate distally in ventral view, irregular or with a concavity (rarely 2) apically in some specimens (figs 2, 3).

Female. Antennal rami on segments 3 to 11, 12, or 13, rami less than half the length of those in males. Forewings with forks 1 to 5 present, forks 3 and 4 on long footstalks, hind wings similar to male (fig. 5). Sternite VIII with a band of short pale setae along posterior margin (figs 6, 7). Genitalia: tergite IX very broad and sclerotised dorsally, narrowly cleft mesally, medial notch on posterior margin. With a pair of depressions laterally on segment, with a weak carina along dorsal margin of each. Sternite IX with triangular sclerotised area on anterior half of segment, fleshy laterally and posteriorly (figs 6–9). Simple, apical lobes fused with segment X or lost.

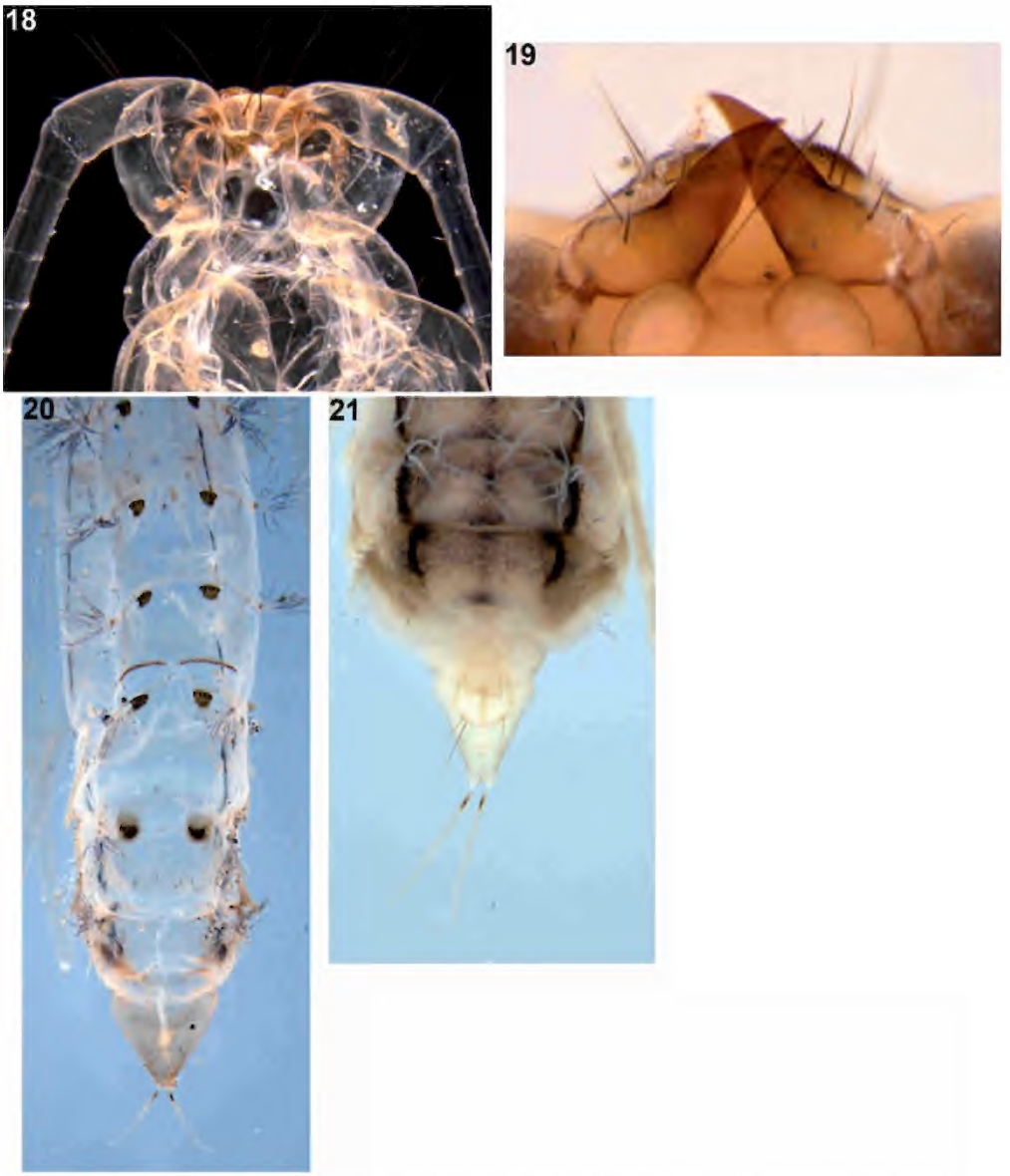
Pupa. Head with a pair of prominent rounded, tuberculate warts on the frons taking up most of the width of the frons which are similar to, but more prominent than, those of *Aphilorheithrus* and *Kosrheithrus*; a pair of long setae dorsally medially on the head between the antennae, a second pair just dorsal to the tuberculate warts (fig. 18), labrum with 3 pairs of setae in each dorsolateral corner; mandibles blade-like in apical half, narrowing to a point, straight and serrate on inner margin, rounded and smooth on outer margin, with a pair of medium length setae basally (fig. 19); each scape with medium length setae, 1 pair mesal dorsal and 1 pair distal ventral (fig. 18). Legs without swimming fringes, rarely a weak fringe on at least one mid leg. Abdomen with pairs of



Figures 5–9. *Ramiheithrus virgatus* female: 5, Kiandra right fore and hind wings; 6, Kiandra genitalia lateral; 7, Sassafras Gap genitalia lateral; 8, Sassafras Gap genitalia dorsal; 9 Sassafras Gap genitalia ventral. d = depression.



Figures 10–17. *Ramiheithrus virgatus* Sassafras Gap larva: 10, head dorsal; 11, head, thorax and first abdominal segment dorsal; 12, head, thorax and first abdominal segment ventral; 13, foreleg anterior face lateral; 14, legs posterior face lateral; 15, abdominal segment IX dorsal; 16, last abdominal segment ventrolateral; 17, case and posterior closure. cs = cluster of setae, pc = particles closing posterior opening.



Figures 18–21. *Ramiheithrus virgatus* Sassafras Gap pupa: 18, shed cuticle head and thorax dorsal; 19, anterior of head ventral; 20, shed cuticle abdomen dorsal; 21, last abdominal segment ventral.

anterior dorsal hook plates on segments 3 and 4 each with 2 to 4 teeth, segments 5, 6 and 7 each with 3 to 6 teeth; pair of posterior hook plates on segment 5 each composed of a row of 16 to 25 spines, many bifid (usually different number on each side) covering most of the width of the segment and with a short gap between each plate, spines as long as plates (fig. 20). Last abdominal segment elongate subtriangular, with 2 pairs of long setae mesally, ventrally (fig. 21). Anal processes as for the family: lightly sclerotised, long, very narrow and slightly curved apically, each with a short dark pigment band close to the apex and without setae (figs. 20, 21). Larval case with anterior pupal closure a disc of silk without any openings holding on a capping stone.

Larva. As for diagnosis. Final instar larva head capsule width across eyes 1.3 to 1.4 mm.

Remarks. Note that the variation found in wing and genitalic structures of the male were found in all populations.

Ramiheithrus kocinus Neboiss, 1974.

Figures 22–23

Type Material. Holotype male: Tasmania. Small creek in forest, Corinna. 5 November 1972. A. Neboiss and G. Kocins (NMV TRI-4567). 1 Paratype collected with holotype (NMV TRI-4568).

Other Material Examined. Tasmania. Creek crossing Gordon River Road. 42.887° S 146.379° E, 11 January 2012, 1 male (LTUT1103-12) (NMV TRI-54701) M. Shackleton and J. Mynott.

Diagnosis. As for the generic diagnosis with the following additions. Male genitalia with segment X median lobe broad, shorter than lateral lobes (fig. 22).

Description. Revised after Neboiss (1974). As for the generic description with the following. Type specimens blackish with faint paler irregular mottling on forewings of which the most conspicuous is a pale area covering cross veins s, r-m and m, and extending along back along M1 about half the length of the wing. Gordon River Road specimen greyish brown with indistinct white mottling and spots, forewing 9 to 9.5 mm long. R2 joining R3 in type specimens only, fork 1 with or without a short footstalk. Forewings of male with vein A2 long in type specimens, short in Gordon River Road specimen (fig. 23).

Male genitalia. Phallus broad apically; segment X lateral lobes with a few moderately long spines medially; inferior appendages come to a slight point laterally (fig. 22).

Female, pupa and larva unknown.

Remarks. This species is known from only two specimens from the type locality and one specimen from a site (Gordon River Road) about 170 km southeast of the type locality. DNA information is only available for the southern specimen. There is some variation in wing colour and venation and male genitalia but with so few specimens available they are considered conspecific for now.

Additional presumed species of *Ramiheithrus*

Larvae found at two localities in the Yarra Ranges National Park are included here and are the only other species known in the larval stage. This enables preparation of the generic diagnosis and description. The distinctness of these two species is based on the genetic distance, as discussed in the preliminary genetic analysis below.

Ramiheithrus sp. 1

Figures 24–25

As for the larval generic diagnosis and description with the following additions.

Description. Larval head capsule yellowish brown, width across eyes 1.4 mm, body length 12 mm. The only mid leg on the one specimen has the remnant tibial spine about 1/3 as long as that of *R. virgatus*; prosternum with pair of small sclerites immediately anterior to the large central sclerite (fig. 24). These characters may not enable separation from larvae of other species when variation within each species is known. *Philorheithrus* larvae also show almost no variation between the three species recognised (Henderson and Ward, 2006).

Material examined. Victoria: Alderman Creek at Track 32, Yarra Ranges National Park, 37.721° S 145.941° E, 5 November 2009, 1 larva, J. Dean and R. St Clair (LTUT721-12) (NMV TRI54435).

Ramiheithrus sp. 2

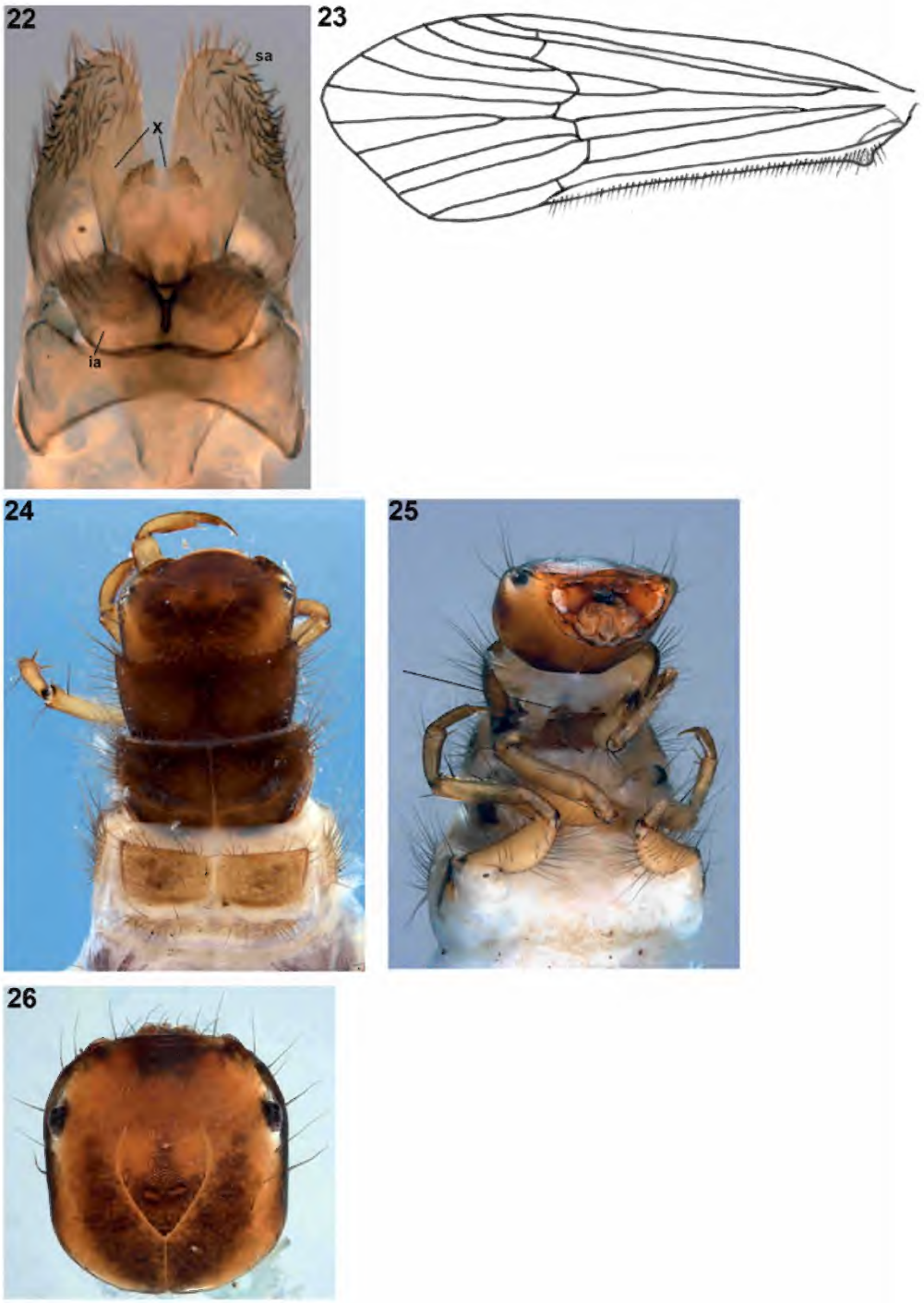
Figure 26

Description. Adult unknown. Larva. As for generic diagnosis and description. Head capsule yellowish brown, width across eyes 1.5 mm, body length 12 mm. Case posterior closure comparatively flat with attached particles smaller and sparser than in the other two species.

Material examined. Victoria: Contentment Creek site ETT4DS R5, CAPIM Black Spur Weir Project, 10 January 2013, 1 larva (LTUT1385-14) (NMV TRI-55176); Contentment Creek, CAPIM Black Spur Weir Project, 10 January 2015, 1 larva (NMV TRI-54816).

Table 1. Specimen details for sequenced *Ramiheithrus*

MV Registration No. (TRI)	BOLD Process ID	COI GenBank Accession No.	BOLD BIN No.	Accession No.	Life stage
54701	LTUT721-12	KX291310	ABV8839	JOS152	Larva
54702	LTUT1385-14	KX296550	ACM3556	EPAVT54	Larva
54437	LTUT720-12	KX296621	ABV9442	JOS151	Larva
54703	LTUT723-12	KX292939	ABV8840	JOS154	Adult male
54435	LTUT1103-12	KX293205	ACC8741	JOS316	Adult male



Figures 22 – 23. *Ramiheithrus kocinus* Gordon River Road male: 22, genitalia ventral: 23, left forewing (rotated 180° for comparison with other wings). Figures 24 – 26. *Ramiheithrus* sp. 1 larva: 24, head and thorax dorsal; 25, head and thorax ventral. Ramiheithrus sp. 2 larva: 26, head dorsal. ia = inferior appendage, sa = superior appendage, X = segment X.

Discussion of COI data

An abbreviated COI taxon identification tree is shown in fig. 27 and information on specimens is provided in Table 1. Only one specimen was barcoded from each of five localities. Usually, at least five specimens over the range of the species are required to confirm genetic distinctness. Thus, more sequencing is required to confirm the current interpretation.

The COI taxon identification tree indicates that the two larvae from the Yarra Catchment (LTUT721-12 and LTUT1385-14) are genetically very different from each other and from other specimens (fig. 27). Because there is no adult specimen available from either locality, these species are not being formally described.

The genetic distance between the specimen of *Ramiheithrus virgatus* from near the type locality (LTUT720-12) and the specimen from near Mt Buller (LTUT723-12) is close to 5%. This is greater than often considered necessary to indicate distinct species. However, no consistent morphological features were found to support recognition of the Mt Buller population as a new species. The generally large distances between all specimens indicate that the commonly applied 2% or 3% threshold for species separation may not apply to this genus. As a result, all the Victorian (apart from the larvae from the Yarra catchment) and New South Wales specimens are here assigned to the one species.

Discussion of larval habitat and its implications

Larvae of *Ramiheithrus virgatus* have been collected for the first time. The first larva collected was in a roadside trickle that is only present after rain and which was dry the day following collection. The trickle appeared as a point where a narrow conduit of groundwater reached the surface, rather than just a point where a broad area of groundwater happened to reach the surface. Investigation found pupae and more larvae in saturated coarse gravel behind a large mound of moss. The seep was less than two square metres on a vertical area of road cutting. Water flowed into the roadside ditch from this area in rainy conditions. This locality was very close to

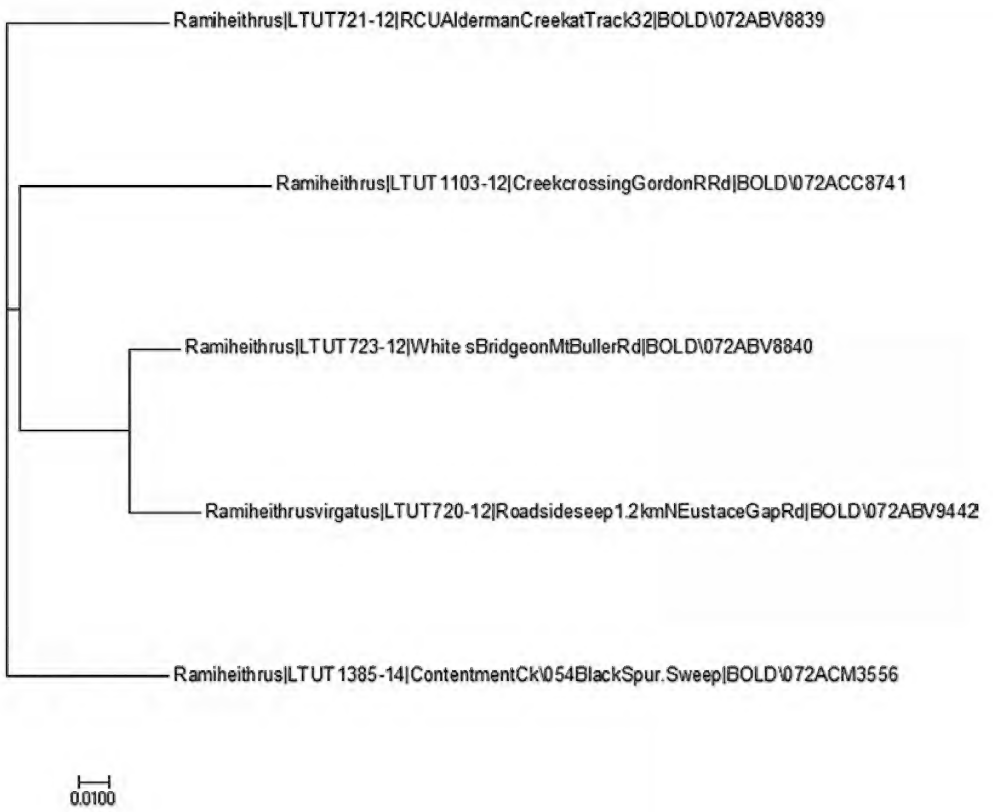


Figure 27. BOLD Taxon identification tree.

the type locality and an adult was collected at light at this new locality soon after finding the larvae and pupae. Some pupae were reared to the adult stage. No similar localities were found nearby, despite extensive searching.

After the habitat was recognised, attempts were made to find similar habitats on the Mt Buller Road, the only other locality in Victoria where adults have been collected. No such habitat or *Ramiheithrus* larvae were found. Areas where ground water was flowing into roadside ditches following rain were found but not associated with a particular moss and not appearing to lead to a gravelly conduit. Presumably, such areas are present but not on the roadside, at least at the time of searching. Being so small, such habitats would be extremely difficult to locate hidden within the vegetation.

The only specimen of *Ramiheithrus* sp. 1 was collected at a standard riverine habitat. However, as only one larva was collected, despite the site being sampled on numerous occasions by the Environment Protection Authority Victoria over a 20-year period, this clearly is not the preferred habitat of the species. This larva was presumably washed in from its usual habitat. A similar but smaller area of moss was noted on a road cutting about 100 metres uphill from the site but not investigated.

The specimens of *Ramiheithrus* sp. 2 were collected from very small trickles, a slightly different habitat to that of *Ramiheithrus* virgatus. Several specimens were collected; therefore, this appears to be their habitat.

The assumption is made that the habitat is similar for all species of *Ramiheithrus.* The fact that only a single larva has been found in a true riverine habitat supports the fact that the main habitat is unusual, and soaks like that where *R. virgatus* was collected near Sassafras Gap are considered the most likely.

Although found in alpine areas, this genus has not been found above 1500 metres. This also could be related to the habitat as it would occur lower down the mountain where ground water seeps out of conduits and associated with a particular type of moss.

The fact that collection of the larvae is so difficult means that species in this genus will be difficult to manage. *Ramiheithrus virgatus* is listed as vulnerable in Victoria and *R. kocinus* is listed as threatened in Tasmania. The adults are rarely found and in low numbers when they are collected. However, E. Riek collected adults at the one locality four times over 11 years. Adult specimens have been collected from the White Bridge locality on more than one occasion, although collecting on other occasions was unsuccessful. It is possible that adults usually remain near the larval habitat. Targeted collecting would be extremely difficult due to the very patchy nature of the habitat.

With the larvae and adults probably living in small areas of habitat spread over a wide area, could this be the reason why adults have rami-bearing antennae. Presumably they have a sensory function. Gao et al. (2016) suggested rami enable greater sensory function for detection of pheromones or volatile chemicals from food. It is possible the rami in *Ramiheithrus* are used to locate other adults in highly localised habitat patches.

The absence of swimming fringes on the mid legs of the pupae may be an adaptation to the larval habitat as the pupae were not collected in free water. At this stage, the pupa of only one species is known so this may not be typical of all *Ramiheithrus* pupae. Examination of pupae from most Australian Philorheithridae genera found they have swimming fringes. One of the two species of Philorheithridae pupae described from New Zealand, *Philorheithrus agilis* is found in swift streams has swimming fringes while *Philorheithrus litoralis* has a very weak fringe of few pale setae and is found in small streams or seepages (Henderson and Ward, 2006).

Two females of *Ramiheithrus virgatus* reared from pupae had many well-developed eggs in the abdomen. This may be another adaptation to the unusual habitat, but because it is not known how many philorheithrid species are similarly advanced when emerging, this cannot be confirmed.

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George Lyell and Frederick Parkhurst Dodd: authority and expertise in nineteenth-century Australian entomology

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Abstract

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This article focuses on the correspondence and careers of two lepidopterists, George Lyell and F. P. Dodd. Drawing on Dodd's unpublished letters to Lyell during the late nineteenth-century rage for butterflying, it examines how private acquisition gave way to the professional activity of collecting and, in Lyell's case, the eventual gifting of a large and significant collection of moths and butterflies to the National Museum of Victoria from 1932 through to 1946. The article also examines how issues of authority and expertise were measured and contested among collectors in this period.

Keywords

F. P. Dodd, George Lyell, lepidoptery, collecting, correspondence, professionalisation, National Museum of Victoria

Introduction

Professionalisation in nineteenth-century life sciences is a lively topic within British and North American histories of science, but it is a topic less examined in the Australian context. This article extends current debates by examining the correspondence between two self-taught Australian lepidopterists, Frederick Parkhurst Dodd (1861–1937) and George Lyell (1866–1951). Both were private collectors, born in the shadow of the Grampians in south-west Victoria, but that is where the similarities end. Lyell built a large collection of Lepidoptera while working full-time in business, whereas Dodd supported a large family through selling his specimens. The article begins with Lyell's decision in 1932 to donate his large collection to the National Museum of Victoria. It then moves back in time to an examination of Dodd's letters to Lyell from 1897–1904. These letters, while reflecting informal one-to-one transactions of exchange, donation and purchase, operate within a much larger push and pull of external factors. These external factors include a wide network of people who were themselves subject to a thicket of protocols, depending on their perceived status within the group. Furthermore, the complexity and interdependence of the various people involved in the science of entomology led to many disputes about who exactly qualified as professionals. Arguments as to who held the most requisite authority and expertise were particularly acute during what has been dubbed the Period of the Amateurs, 1890–1930 (Mackerras, 1949).

The George Lyell collection

In March 1946, Richard Pescott (1905–1986), Director of the National Museum of Victoria, informed the Australian Broadcasting Corporation's Melbourne office that the first instalment of a magnificent collection of Australian butterflies and moths was about to be exhibited in the main hall of the museum on Russell Street. The collector was George Lyell (1866–1951; fig. 1), and his gift to the museum was so large that it had to be exhibited in relays, from 1 April 1946 until mid-year. The announcement contained an overall description of the collection as well as information gleaned from an interview with Lyell about his gift to the state of Victoria. Although the whole appeared under Pescott's name, the real author was journalist and naturalist Charles Barrett (1879–1959). After the Australian Broadcasting Corporation published the piece, Barrett then circulated it to *The Herald*, *The Sun*, *The Age* and *The Argus*.

We learn from Barrett's interview that Lyell had decided to donate his collection after suffering a serious illness in 1932. In the 14 years since then, he had devoted himself to the colossal task of preparing more than 50 000 individual specimens for the handover, remounting and resetting many of them in the process. His aim was to build for the museum "the most comprehensive collection of Australian moths and butterflies ever known". At the time of Barrett's writing, the collection numbered 51 216 specimens, consisting of 11 721 butterflies and 39 495 moths, representing 6177 species all told. World-renowned authorities had already named 534 type

specimens, but new species were still being discovered and named within the collection. In addition to praising Lyell's great scientific knowledge and technical skill, Barrett emphasised that the gift had been unconditional, Lyell having taken the "broadminded scientific view" to amalgamate the Museum's collection with his own. In this way, gaps would be filled, ensuring that the collection would be "truly representative of Australian entomology". Barrett concluded with a brief overview of the collection's highlights, such as the "particularly beautiful" swallowtail butterflies and the "lovely Blue butterfly, *Papilio ulysses*". It was in the moths, however, that the collection approached perfection (Melbourne Museum, Notice to Manager, ABC, AB 576, 29 March 1946).

Lyell was born at Ararat, Victoria, in 1866, the fourth of eight children (Hewish, 2014). His father was a printer born in Scotland and his mother was English. Apparently, he showed little interest in natural history until he caught his first butterfly, a caper white, at Albert Park in 1888. Wanting to know more about this creature, the 22-year-old contacted Frank Spry (1858–1922) who immediately introduced him to the Field Naturalists' Club of Victoria, which was founded in 1880. While attending meetings regularly over the course of

Figure 1. George Lyell as a young man.

the following year, Lyell continued to collect at Albert Park, where he distinguished himself by collecting 13 lesser wanderers, a butterfly that had not been recorded in southern Victoria for well over a decade. He also made occasional visits to other well-known hunting grounds: Murrumbeena, Springvale, Hampton and Cheltenham.

In 1890, Lyell moved to Gisborne in central Victoria to work as bookkeeper for the town's largest business, Cherry & Sons Pty. Ltd., timber merchants and manufacturers of dairy equipment. Later, as Lyell rose to Manager and then Director, the firm developed an export business in entomological supplies such as nets, mounting boards, pins, forceps, cotton wool, boxes and cabinets (Hewish, 2014). Here, in this small country town outside Melbourne, Lyell lived for the rest of his life. His collecting was confined to Victoria and New South Wales, except for one trip each to South Australia, Tasmania and southern Queensland. Nevertheless, he corresponded and exchanged Australia-wide with scores of notable entomologists such as A. J. Turner and R. Illidge of Brisbane, G. M. Goldfinch of Sydney, G. B. Lower of Adelaide and F. P. Dodd of Kuranda, north Queensland. He also co-authored, with G. A. Waterhouse, *The Butterflies of Australia* (1914). This extensive exchange network across Australia resulted in long series of individual species, a notable and highly valuable scientific feature of Lyell's collection.

In outlining Lyell's career, Barrett paid particular attention to Lyell's triumph over the largest obstacles facing collectors, namely housing his collection and protecting it from the scourges of pest infestation and mould. Lyell achieved this by devising a small display cabinet of six or eight drawers, constructing it in such a way that each subsequent unit could be fitted together to make more cabinets, similar to the way in which a bookcase might be enlarged. In the 1890s, at the start of his collecting career, Lyell could only afford to build one of these cabinets annually, but by 1932 he owned more than fifty, built by Cherry & Sons. What Barrett did not know, or chose not to disclose, was that Lyell had approached Sir Macpherson Robertson in 1934 for £500 to build the many extra cabinets he needed to house his gift. Robertson, founder of the MacRobertson Confectionery Company in the Melbourne inner-city suburb of Fitzroy, was one of Australia's richest and most successful businessmen. Whereas Cherry & Sons struggled after the Depression, business remained strong for Robertson who contributed generously to the upcoming centenary of Melbourne's founding in 1835, including a substantial donation towards the building of the city's herbarium. In essence, Lyell asked Robertson to do for Australian Lepidoptera what he had recently done for botany. Signing off anonymously as a collector and fellow-Scot, the normally modest Lyell took the opportunity to boast that his collection would be "an object lesson to all the museums of the world and a lasting scientific attraction to Melbourne". Lyell finished by inviting Robertson to make enquiries of the Museum Director, D. J. Mahony, an invitation promptly taken up by the confectionary magnate (Melbourne Museum, Archive Box 579, 27 December 1934). In his response, Mahony revealed Lyell's identity and confirmed that a shortage of money was indeed hampering the progress of his gift. In praising the collection as "the best of its kind", Mahony described the meticulous way in which Lyell cared for his insects. Not only did he perform yearly stocktakes to check on their condition, he also compiled annual balance sheets showing acquisitions, as well as insects discarded or exchanged. Mahony confirmed that "Every specimen is therefore fully documented" (Melbourne Museum, Archive Box 579, 9 January 1935). In the end, Robertson declined to support Lyell, arguing that he had already over-committed himself in support of the city's centenary.

George Lyell and Frederick Parkhurst Dodd

When interviewing the elderly Lyell in 1945, Barrett asked him which was the favourite of his 6177 insect species. Lyell at first parried the query, declaring "you have set me a poser. They are all beautiful". In the end he confessed that it was the Queensland wood moth *Dudgeonea actinias* Turner, bred "from a rotting log in a creek bed at Townsville" by Frederick Parkhurst Dodd (fig. 2). In 1903, Cyclone Leonta buried the log under 30 feet of flood debris. Of the 13 specimens bred by Dodd, seven are in the Lyell collection (fig. 3). While Dodd was just one of Lyell's many Australian correspondents, we know a lot about their relationship because there is an extensive run of letters from Dodd to Lyell in the Melbourne Museum archive. Although, unfortunately, Lyell's letters to Dodd do not appear to have survived, the correspondence reveals the many interdependent players and complex processes at work in shaping the Australian entomological community during the late nineteenth century.

The collecting, exchanging and selling of insects was serious business in the years leading up to Australian Federation in 1901, evident in the brisk and lively circulation, both locally and internationally, of collectors, publications, specimen boxes and letters. Given the enthusiasm for Lepidoptera, there was serious money to be made, especially on large and brightly coloured tropical specimens. The story of Conrad Kelsall, an English immigrant farmer who settled in the rainforest of north Queensland, is instructive. Within four short months in 1903, we see the rise and fall of Kelsall's hopes for a tidy profit from butterflying on the Little Mulgrave River. In letters to his sisters back in Devon, he began with great confidence, declaring his tropical home as "so new & unexplored that one is almost certain of making new finds". With the help of an indigenous man nicknamed Paddy, who captured about a dozen males of the large birdwing butterfly *Ornithoptera euphorion* Gray, Kelsall asked 6d for each of them from Alfred Bell, an insurance agent and butterfly enthusiast based in Cairns. Later, for a box of 100 butterflies, Bell paid Kelsall 25/–, proposing that, instead of cash transactions, his profit would double if he agreed in future to "run on halves" and "take some risks". Once the business was "in full swing", Bell envisaged that similar boxes might average out at "£3 or £4 per hundred". Although new to the collecting business, Bell boasted international contacts with the famous lepidopterist Walter Rothschild, as well as with Watkins and Doncaster, the English natural history dealers. Bell was also supplying insects to Lyell and Waterhouse in Sydney, at that time preparing their catalogue of Australian butterflies. But within a few months, Kelsall confessed to his sisters that he

and his business partner needed "to modify our castles considerably". After failing to catch anything in an expedition to Lake Barrine, they returned to discover that all but 14 of the 100 insects they had sent to the Australian Museum had been rejected. Worse was to come in the shape of an insulting and caddish letter from the English dealers who purchased only two of the butterflies sent over. Claiming that the rest were too damaged, they promised to return them all to Queensland but no box arrived, leaving Kelsall to conclude, ruefully, that "it is easy swindling a person 12 000 miles away" (Lambkin, 2013).

While Kelsall was one of many minor part-time enthusiasts, Frederick Parkhurst Dodd is now regarded as a leading Queensland collector. Born in Wickliffe, Victoria, one stagecoach stop from Lyell's birthplace in Ararat, he was the son of a pound-keeper and the eldest of eight children (Monteith, 1991; Neboiss, 1986). After the family moved to Stawell, on the edge of the Mallee, Dodd was educated at the same local state school as Lyell. Here the similarities stop. While Lyell went on to lead a settled life in a rural town within easy reach of Melbourne, Dodd joined the bank in Victoria and was then shunted around to various bank jobs in Queensland, starting in remote Townsville in 1884. He never returned to live in Victoria. Apart from six years in Brisbane, where he met and learned much from a number of prominent entomologists connected to the Queensland Museum and the Natural History Society, Dodd's early life as a bank clerk took place a long way from the metropolitan scientific societies of Brisbane, Melbourne and Sydney. Eventually, hating the confinement of office work, and determined to become a full-time collector, he left the bank and eventually settled in 1904 in Kuranda, a tiny town on the Atherton Tableland. The area was rich in insects, but all his entomological books and journals had been destroyed by Townsville's Cyclone Leonta the year before. In Kuranda there were no local libraries and no entomological societies or meetings in which he could participate.

In Dodd's letters to Lyell, we see the value, and indeed the necessity, of correspondence that connected him to Melbourne's scientific and collecting community, including the Victorian Field Naturalists' Club and the National Museum of Victoria. Lyell kept Dodd connected to professional societies and their activities, including access to the all-important journals. Membership of these societies and subscriptions to their publications were expensive, often beyond Dodd's means, but when business was good, he turned to Lyell for suggestions as to who might propose and second his admission. In addition to Waterhouse and other prominent entomologists at the Australian Museum in Sydney, Lyell counted Walter Froggatt (1858–1937) as a friend. Founder of the Naturalists' Society of New South Wales in 1891, Froggatt published regularly on Australian entomology in

Figure 2. *Dudgeonea actinias* Turner.

the *Proceedings of the Linnean Society of New South Wales*. After Froggatt was appointed government entomologist to the New South Wales Agricultural Department in 1896, Dodd asked Lyell to mention him in case the Department wanted to purchase some of his specimens (Museums Victoria Archives, OLDERSYSTEM~03023, AB 00368, 24 March 1901).

Dodd's correspondence with Lyell is rich in self-description, shedding light on the so-called divide between mere collectors and entomologists. The label of mere collector had been hurled by Gerard Krefft, controversial Curator of the Australian Museum, at William John Macleay during a parliamentary investigation into the museum in 1874 (Ville, Wright, and Philp, 2020). Although this divide between the true scientist and the mere collector was more rhetorical than real, it was deeply embedded in nineteenth-century thinking about who exactly possessed the authority and expertise to speak for entomology. In 1838, the British entomologist John Obadiah Westwood (1805–1893) described as the very "lowest class of entomologists" those "whose sole object is the procuring, either by capture or by purchase, of a collection of handsome insects, to be placed in drawers without any arrangement other than that of beauty and colour or size" (Wale, 2019, pp 405–406). As an insect breeder and naturalist, Dodd was far from this lowest class. His deep knowledge of the bush around him and pride in his technical skills are clear in his letters, which are full of observations about the habits and life histories of insects—their location and distribution, their food plants, their relationship to other species and genera, their enemies and their mechanisms for self-defence. Many of Dodd's fine-grained observations stemmed from tireless watching of the insects with which he lived intimately, both at home in breeding boxes, in the bush beyond, and in his Kuranda garden, planted with especially chosen flower and tree species.

Despite his expertise, it is notable that Dodd never describes himself as an entomologist. Instead, his insects are "entomological material" and he himself is a "worker in Entomology". He even apologised to Lyell in his first letter for addressing him as entomologist on the envelope, explaining that he wanted to ensure the letter reached him (December 1897). There are several explanations for why Dodd refused to call himself, or anyone else he admired, an entomologist. The first reason was his dislike of the entomological fraternity: "I have a very poor opinion of Entomologists generally", he tells Lyell. In particular, he had little time for the growing number of sedentary and salaried museum men whom he regarded as far less knowledgeable and skilful than himself. Writing to Lyell in 1901 about J. A. Kershaw (1866–1946), later curator and then Director of the National Museum of Victoria, Dodd places him contemptuously amongst the "amateur Entomologists", with the word "amateur" doubly underlined for emphasis (National Museum of Victoria, 15 July 1901). The reason for his dismissal of Kershaw and others stemmed from his pride as an insect breeder with first-hand eye-witness experience. Even Froggatt, author of *Australian Insects* (1907), the first comprehensive textbook on Australian entomology, failed to come up to scratch in Dodd's opinion. While he conceded to Lyell that Froggatt "may be a good entomologist" he added that "he had better drop writing the life histories of moths". According to Dodd, Froggatt had been duped by a Newcastle collector called Thornton into believing that the larvae of *Endoxyla encalypti* had bored as deep as five feet into the wattle tree roots, "high class rubbish" that had been published in the *Proceedings of the Linnean Society of New South Wales* (National Museum of Victoria, 1 January 1898). Elsewhere, Dodd refers to Froggatt (anonymously) as "an Australian Munchhausen" for producing the same exaggerated observations (Dodd, 1916).

Keen to read the latest essays, notes, and pamphlets about insects, Dodd published some important discoveries of his own in entomological and natural history journals, both Australian and international. Geoff Monteith gives two examples of the ways in which Dodd was ahead of his time in understanding the life histories of insects. Dodd is now known for his breakthrough insights into the symbiosis between green tree ants and the highly prized butterfly *Liphyra brassolis* Westwood. Also notable was his detection of the mimicry between the rare swallowtail butterfly, *Papilio laglazei* Depuiset, and the poisonous day-flying moth, *Alcides agathyrsus* Kirsch (Monteith, 1991). However, with no access to large reference collections and short on time, Dodd was, as he confessed to Lyell, "but poorly acquainted with the names of our [Australian] insects" (National Museum of Victoria, 11 October 1897). A few months later, having picked up on the fact that Lyell was "well posted in the names", he asked him for help, confessing that

> unfortunately hundreds of my species are yet unknown to me by name. I shall do all I can to get them identified + hope to get a list compiled such as yours. When furnishing particulars of specimens sent, or even acknowledging exchanges, can you kindly add names of sub family + family of individual specimens; in many cases the generic name + view of the moth does not tell me what the insect is (National Museum of Victoria, 11 December 1897).

Before long, he was thanking Lyell for the trouble he had taken in supplying him with names (National Museum of Victoria, 12 February 1898).

Dodd's failure to master the precise names of insects did not mean that he despised the systematists. In fact, he was extremely proud of the great attention shown to his collection by Brisbane-based Dr Alfred Jefferis Turner (1861–1947), an expert in classification who would often travel to Townsville, and later Kuranda, to study, describe and name Dodd's insects (National Museum of Victoria, 29 September 1900). You can hear Dodd's pride in a comment he made to Lyell of a small syntomid he sent on to him. Turner, he wrote, regarded the specimen "as a great prize, and in fact he thinks very favourably of all the kinds I am sending you. He often calls upon me, to examine my collections, + learn if I have anything fresh in the way of captures, or from my breeding boxes". Rowland Illidge, Dodd's mentor during his years in Brisbane, was another expert identifier, helping him to name hundreds of species. Despite his self-confessed deficiencies in this arena, Dodd was never cowed. When Lyell returned a large hawk moth, believing it was not the moth Dodd had promised

him, Dodd exploded with irritation. In this instance, where the differences between species were scarcely perceptible, Dodd's experience as a breeder gave him that extra degree of self-certainty (National Museum of Victoria, 27 May 1901).

On balance, rarity was a strong possibility in the remote Queensland tropics, but how could Dodd always be certain, lacking expert associates and reference materials? Perhaps his rare insects were common elsewhere? Furthermore, in several letters, responding to Lyell's doubts about identifying a particular specimen, Dodd asked him to "refrain from getting fresh species named" until he had corresponded with Turner on the matter. If the insect was indeed rare, Dodd could only get full credit for the discovery after Turner's identification. More often, to his regret and frustration, he confessed to Lyell that he

> carelessly sent away unnamed things, perhaps some reared with great care + trouble, to find some day that they have been described from "Somebody" collection, having been taken or bred in Queensland!! This is very annoying to me. I have bred more Zeuzeridae than anyone living or dead, and my name is never mentioned in connection with the new things. Also I have bred more Charagiae [*Aenetus*] than anyone else. As to Xylos I have bred over 50 species in north Q'land, including those I got at Charters Towers years ago, perhaps 60 species. I don't know how many species I bred in south Q'land (National Museum of Victoria, 26 November 1900).

Clearly, Dodd resented the anonymity that came with living so far away from the centres of entomological research. Given the toil of collecting rare and elusive insects, this was understandable. Why should others, often wealthy purchasers, be given the credit for his work? This sometimes made him quite vain about being acknowledged for the discoveries he had made. In a letter of June 1898, he followed up with Lyell on one of his moths: "Oh, when getting that beautiful Oecophoridae named did you credit me with breeding it? I have <u>one</u> left and Dr Turner was charmed with it" (National Museum of Victoria, 9 June 1898). At other times, however, he begged Lyell to conceal information about what and where he was collecting. The wish to be acknowledged for the very details he needed to conceal reveals the painful bind in which he found himself (Monteith, personal communication, 6 July 2018).

Lyell understood his correspondent's dilemma and was happy to observe the friendly protocol of sending all queries about names to Turner before consulting anyone else. In return, Dodd made a point of impressing on Lyell how much he trusted him. For instance, Dr Turner was, he told Lyell, anxious to name one of his insects as new but he only had two specimens, one of which he had sent to Lyell. "No other collector would have done that", he declared. Nevertheless, Dodd's inability to name insects scientifically remained something of a sore point, leading him many years later to pronounce, defensively, to J. A. Kershaw:

> It is too severe a <u>mental strain</u> for a professional collector to attempt to learn the names of the thousands of insects which pass through his hands, so I seldom can supply names . . . Years ago I had a long list of names of Lepidoptera, but lost it in the Townsville cyclone. I could not replace it, a busy life of collecting has prevented my endeavouring to make another.

Dodd's boast was that he possessed other skills, such as his detective work in locating and hatching out insects, then setting them perfectly, reminding Kershaw at the end of his letter: "I can send nicely set bugs ants &c &c if the Mus[eum] cares for same" (National Museum of Victoria, 1 June 1911).

Building Trust

Dodd's first letter to Lyell, dated 9 September 1897, enquired if he might be included in his circle of "exchanging correspondents" (National Museum of Victoria, 9 September 1897). Dodd had often seen Lyell's "nicely set insects … perfect in every way" in Queensland, so he was confident that their exchanges would not just be rewarding but (even more importantly) equal. A perfectionist, Dodd often complained about the low standards of others. In fact, he told Lyell he did not want Melbourne entomologists to know that he had a large number of insects for exchange, his reason being that "several of them do not set well enough to please me + as a rule I get inferior material to my own". Kershaw, for instance, had proved disappointing, palming off on him "faded, damaged, or common specimens" for the "rare or beautiful things" he had been sent. Lyell was probably sympathetic; like Dodd, he was proud of his meticulous standards of preservation and mounting. Notably, although Barrett would later describe Lyell's gift to the National Museum as unconditional, there was, in fact, one condition. When it came to amalgamating his collection with the Museum's, Lyell stipulated that his own was to take precedence. While anything worth saving from "the smaller and poorer old museum collection" would be remounted for inclusion, he demanded that most of the museum's specimens be scrapped (Melbourne Museum, Archive Box 579, 27 December 1934; Lyell to Robertson).

Despite Lyell's meticulously high standards, Dodd soon found cause to chastise him for the arrival of 26 damaged specimens, including some with "one or both antennae broken and missing". Suddenly, the mutual trust and reciprocity that was to cement their relationship was threatened. The geographical balance and complementarity that Dodd was seeking between Victorian and Queensland specimens was also jeopardised:

> In looking through the exchange lately received I regret to notice that many of the specimens are imperfect, or rubbed, and others seem rather old. You may remember my request for clean and perfect insects, and I trust future lots will be a great improvement on this … I have a large collection and the condition of same is first class. I keep no damaged specimens that I can replace with perfect ones and I am sorry to say that my Victorian collection compares very

> poorly with my own; in fact they spoil the appearance of the others. Therefore I want no more damaged things and no matter how rare a species is, please do not send it to me unless perfect in every particular. I cannot prize a thing with a great gap or gaps in its wings, antennae missing, or badly rubbed &c &c. Should you care to continue these exchanges may I hope that you will kindly place me upon your first class list … (National Museum of Victoria, 12 February 1898).

Behind Dodd's fastidiousness lay the fear that Lyell was not taking him seriously enough. Perhaps Lyell regarded him as a mere collector? This anxiety is evident in the way in which the adjective *first class* shifts in this paragraph, from the insects in Dodd's collection to the list of Lyell's correspondents. Keen to reinforce his standing as a first-class collector with a first-class collection, he reminded his Melbourne correspondent of the abundance he enjoyed as a tropical collector. Unlike many who were obliged to capture "almost everything that flies", he had the geographical advantage of refusing hundreds when out in the fields. The spectre of being branded as a mere collector, isolated from professional networks, also prompted Dodd to say that, should anyone enquire of a particular insect, then

> perhaps you will have it mentioned they are in collections Lyell et Dodd, not taken by me as if I was a mere collector. I fear there is an impression abroad that I want specimens for others and not myself and that that is why I "haggle" for only first class specimens, should therefore you have any such impression pray dismiss it.

In other words, Dodd wanted it to be known that, instead of collecting insects solely for exchange, he was proud to retain many of the most perfect and beautiful insects for his own collection (National Museum of Victoria, 16 July 1898).

This early rupture was soon healed when Dodd received a parcel whose contents were "perfect in every way". Writing to thank him, Dodd made no apology for being fastidious. In fact, as if to underline the absence of any apology, he added bluntly that Lyell's new parcel contained "several common things" he did not want. These he would return straight away. Unable to resist reiterating the point about tropical abundance, he had to concede, in fairness, that he was able to catch more in 24 hours than Lyell could catch in five days, but that discrepancy did not mean he had to accept "poor or broken things from a Victorian collector". Nevertheless, the relationship was important to him so that meant an on-going commitment to the delicate task of building trust and reliability. When Lyell received a rare and expensive butterfly, *Ogyris genoveva* Hewitson, and one of its antennae was missing, Dodd insisted that the specimen was absolutely perfect when despatched from Cairns; nevertheless, he immediately sent a damaged specimen with "one good antenna to replace the lost one" (National Museum of Victoria, 26 October 1900, 26 November 1901). As part of the rules governing their exchange, Dodd also assured Lyell that he could return anything he did not want for credit.

This gentlemanly exchange of first-class specimens continued for another couple of years until August 1900 when Dodd informed Lyell that altered circumstances meant he was unable to continue indulging in this pleasurable pastime. With a growing family and a costly relocation from Brisbane to Townsville – a place of "higher prices for everything" – he must now leave off his gentlemanly pursuits (National Museum of Victoria, 27 August 1900). To Kershaw, whom he hoped would purchase insects for the National Museum of Victoria, he wrote that instead of gracing his friends' cabinets, he must now look upon his "beloved specimens … from an £8 point of view". "Most of my best things are reared", he boasted, adding "I keep no rubbish, and no one need fear at any time that I will victimize my correspondents". Despite the taint of trade – making dollars – Dodd nevertheless insisted that his business was an honourable calling. Furthermore, he would keep himself at arm's length from commerce by employing an agent (National Museum of Victoria, 17 September 1900, 31 May 1901). By 1904, he declared that "business with the dealer fraternity is so unsatisfactory" that he was badly in need a larger pool of reliable correspondents. Dispensing with middlemen, he now preferred to deal directly with collectors and museum personnel (National Museum of Victoria, 4 May 1904).

Once Dodd had turned commercial dealer, he encountered a host of rules and protocols governing selling, buying and gifting. These activities were linked, not just to questions of honour and trust between correspondents, but to perceptions of social class and educational background (Lucas, 2013). There was, for instance, the delicate matter of promising certain correspondents first option on rare or large insects. So great was the offence if these sought-after insects were subsequently seen in others' collections that, if Dodd was planning to initiate a new contact, he would first ask permission from his established correspondents. It was also bad form to share the secret of a special location without seeking permission. For instance, Dodd claimed to be the first to let his mentor Rowland Illidge into the secret of where to find two species of the extremely valuable *Aenetus* (*A. ramsayi* Scott and *A. lewinii* Walker) outside Brisbane. To Lyell he divulged: "I was the first in Queensland to find and breed these and at once informed Illidge and we several times went out together. I went away for 12 months + he took [Reggie] Relton into 'mateship' without consulting me". Illidge had also found *Aenetus* exuviae when out in the bush on his own and not let on to Dodd about his discovery. Finally, Dodd liked a correspondent to give full details of unusual insects. When it came to conveying such information, Oswald Lower, a pharmacist in Broken Hill, was one of the very slim ones, he complained. Lower also offended Dodd by lacking an eye for beauty. The closest he got to praising Dodd's settings, or a particular insect, was to ask him to "send another pair". Instead of such obliquity, Dodd preferred directness. He liked correspondents "to express pleasure over a beauty or a rarity": "I get quite cross when I send away a lovely thing if the receiver does not 'enthuse' a little". Lyell must have remonstrated over these complaints about Lower and others

because Dodd conceded: "You are right, biz is biz and I should get all I can. As a seller it matters nothing to me what the buyer is like, I suppose (National Museum of Victoria, 12 August 1901, 6 July 1904).

As a commercial dealer Dodd touted his insects via several selling points. Rarity, beauty and large size were chief. So too, as we have seen, was endorsement by an expert classifier like Turner. The other selling point was his talent as an insect breeder. When circulating sale lists with prices, some pages contained a banner heading stating that all specimens had been bred. In particular, he was proud of his high-priced things, such as his Xylos, stuffed wood-boring moths, bred and reared by him. In his eyes these Xylos were perfect in every way. With every skerrick of fat scrupulously removed, they were (he boasted) very unlikely to turn greasy (National Museum of Victoria, 17 September 1900). Dodd's letters also contain detailed descriptions of his breeding routines. Sometimes he would watch all day until late at night for a large and rare wood-boring moth to hatch. Then, sleeping only for a few hours, he would wake to find his vigilance had been in vain: his valuable moth had emerged and rubbed its wings. Moths in the "restless" but "handsome" family of Notodontidae were particularly prone to offend in this regard, often emerging after he had retired (National Museum of Victoria, 24 March 1901). It was necessary to keep vigil in the bush as well, tending the larvae of insects for years before cutting and transporting the timber home for closer monitoring on the eve of emergence. Sometimes, to Dodd's chagrin, local aboriginals ate the grubs he was watching over. That these grubs were a traditional and highly nutritious food source for Indigenous people cut no ice with Dodd. He was always very testy in his letters when mentioning this so-called theft of his livelihood. His son Walter D. Dodd (1891–1965), also a naturalist, understood better than his father the symbiosis between Indigenous people and country. From Walter Dodd's observations, it was clear that customary ways of living on country entailed a balanced economy of nature. Writing about some very large wood moths he had caught south-east of Perth in 1912, he noted that "The blacks were very fond of 'the grub'". Captive to the prevailing discourse surrounding the "inevitable dying out" of the Aboriginal race, Walter Dodd added that since indigenous people had become extinct in certain localities, "whole patches of wattle forests were laid low, there being no check upon the breeding of these insects" (*The North Queensland Register*, 13 April 1935).

The highest priced moth Dodd ever offered for sale was *Aenetus mirabilis* Rothschild, a species found only in north Queensland (fig. 4). His excitement at sourcing this large moth can be heard in his warning to certain favoured correspondents to "save up your pennies" for a pair (National Museum of Victoria, 26 November 1900). He had read about this moth in a journal article published by Walter Rothschild in 1894, in which the location was disclosed as Cedar Bay, North Queensland. This was a very remote spot 40 kilometres south of Cooktown and accessible only by boat or by foot (Rothschild, 1894). Dodd spent weeks and "a great deal of time and trouble" searching for this moth, at a cost of over £60, so he was obliged to charge highly for it. He assured Lyell, one of the first collectors he contacted regarding his precious discovery, that *A. mirabilis* was unlikely to be found in private collections, or even in the British Museum or any Australian museum "for many a long day, unless through me". As for Lyell's hint that the Victorian Government's entomologist Charles French (1842–1933) owned an *A. mirabilis*, Dodd was dismissive, imagining that it must be a damaged specimen, not perfect like those now in his possession. He asked that Lyell keep quiet about his discovery as demand for specimens was going to be strong, and Dodd wanted to prioritise overseas collectors because they would pay considerably higher prices than those fetched in Australia.

At first, Dodd asked Lyell for 60/– to 100/– [£3–£5] per pair for *A. mirabilis*. This approximates to a price range of £350–£585, or AUD $660-$1100 in today's purchasing power, the wide range reflecting the size, condition and appearance of the insects. Dodd believed this price range was fair and reasonable. His justification lay in the relative pricing of *Aenetus ramsayi*, a species of *Aenetus* that he had managed to sell to English collectors for £4–£6 per pair, even though this moth had been known for a long time and was well distributed, unlike the rare and "very fine" *A. mirabilis*. *A. ramsayi* was also smaller than *A. mirabilis*, the female of which averaged wing spans of 6.5 inches. In the end, Dodd settled on a lower quotation of 55/– to 75/– per pair for Lyell, reducing the cost a little because he realised his friend would find it impossible to obtain such rarities if he "stuck at their money value". He asked Lyell not to mention this discount as he also planned to sell to his competitors (i.e. Australian collectors he disliked such as Lower, a member of the questionable dealer fraternity; National Museum of Victoria, 26 November 1900). Charles French was another he distrusted, telling Lyell that French had the nerve to ask for his precious Xylos but still hadn't sent on the beetles he owed him (National Museum of Victoria, 17 March 1901). Lyell, on the other hand, belonged to Dodd's category of reliable correspondents. In fact, so reliable was Lyell that when, a few months later, wealthy clients had failed to send on remittances, Dodd asked him to pay up-front before he had even despatched the specimen box (National Museum of Victoria, 4 February 1901). He also asked that Lyell pay him a little every month to help keep him afloat between transactions.

When it came to selling his *A. mirabilis*, Dodd pitched his highest price to Lower – £5 for a single pair. In the end, he sold him a pair for £4, a price that he claimed pleased Lower very much. Dodd himself was happy with the transaction. Given Lower's wide network and authority in the field, this sale would prove a good advertisement for Dodd's insects (13 June 1901). In general, Dodd figured that it made good business sense to sell his *A. mirabilis* cheaper to Australian correspondents because this would advertise the perfection of his preservation techniques. Despite this, Dodd held himself aloof and was never less than testy with most of the dealer fraternity, believing that his southern brethren were all down on him because, after 1900, he would only sell and not exchange his grand tropical species for anything they could supply (National Museum of Victoria, 12 August 1901).

Conclusion

In July 1910, G. A. Waterhouse travelled from Sydney to the Atherton Tableland for a week of collecting. Staying in the Kuranda Hotel, he spent a good deal of time with Dodd and his family who were warmly hospitable. From here, Waterhouse wrote to Lyell, describing his first impressions of Dodd. There was much to like about the man. He was clearly an immensely enthusiastic collector who generously lent his sons to visitors like himself for collecting trips. He was pernickety, though, a charge that Dodd would have been proud to acknowledge. In running his business, however, Waterhouse declared him unmethodical, with barely one per cent of his pinned insects labelled with dates. Where there were dates, he suspected that they were a "mere matter of recollection". His classifications were sloppy too, with "similar groups of insects … mixed up anyhow" (National Museum of Victoria, AB 369; 17 July 1910). From Dodd's correspondence with the English dipterist Colbran Wainwright in the same year as Waterhouse's visit, this somewhat cavalier attitude about details can be seen in his postscript to one specimen box: "The localities are roughly marked off on the lids of the cigar boxes. The next lot will be arranged better, and month of capture given" (Royal Entomological Society, 24 August 1910).

As Waterhouse's week in Kuranda neared the end, he informed Lyell that Dodd's "tourist business brings the most money" meaning that "attention to scientific detail suffers in consequence" (National Museum of Victoria, AB 369; 17 July 1910). By tourist business, Waterhouse was referring to Dodd's recent commercial initiative: the opening of his house to members of the public for an entrance fee. Before 1910, Dodd had always welcomed visitors curious to view his collections and see him at work, setting and preserving his specimens, but with entomology a full-time business for supporting his large family, he decided to charge a fee for this. Here we see him in a three-piece suit, posing in his garden with a butterfly net for one of his paying tourists (fig. 5). Dodd was quite the showman in this new business venture, an empresario who used special lighting effects and other tricks to impress his visitors with the mystery and beauty of his insects, turning his home into a semi-

Figure 4. *Aenetus mirabilis* Rothschild (female).

Figure 5. F. P. Dodd in his garden at Kuranda. Image courtesy of Queensland Museum.

public commercial site and museum. Into sober, scientific scrutiny, he injected an older element of spectacle and magic, performing his insects with dramatic exhibitions which mingled natural science, wonder and magic. This was the case even when his visitors were some of the top people in the field, such as Walter Baldwin Spencer and A. J. Gilruth, who visited in 1911.

Margaret Fountaine (1862–1940), a globe-trotting British lepidopterist who had recently settled with her lover not far from Kuranda, left her own account of calling to see Dodd's collection in 1916. Waiving the usual admittance fee of one shilling each, Dodd greeted them heartily as fellow entomologists, and they had a delightful time taking tea and revelling in his exhibits. Fountaine was impressed by Dodd's knowledge of Britain's scientific scene. He had read her articles in the *Entomologist* and in the *Transactions of the Entomological Society of London*. After talking entomological shop for a while, Dodd tried, with a "shrewd, penetrating" look, to dissuade Fountaine from thoughts of farming in the area. He argued, as others had done, that her prospects of success were dim. As she left, she invited him to come over and see her Malay and Java butterflies, an idea that seemed to delight him, but it would not be for a week or so (he claimed) because he was so busy. Fountaine's diary entry concludes:

> We both liked Mr Dodd very much, and I believe the old man wishes to be a good friend to us, especially as he sees that we are not going to be in any way rival dealers, which naturally, as he makes his living out of this business, he could not be expected to look upon with any favour (L. Joanne Green, personal communication, 30 June 2019).

Fountaine's own eye was shrewd and penetrating in concluding that their reception would not have been so friendly had they planned to set up as business competitors.

We have seen Dodd move from exchange to commerce, transacting a business in which there were no fixed prices to guide him in determining the value at which he should trade a specimen. Beauty, colour, size and rarity were key determinants of cost, but perhaps most important was the symmetry and neatness of the setting, allowing the specimens' natural attributes to be seen. Since he was well known for his personal skill in preserving specimens, he believed his reputation in this regard entitled him to charge extra. At first Dodd is uneasy about his new dealer persona, embarrassed to be treating his insects as commodities instead of exchanging them for pleasure. He also worried, at the outset, that seasoned dealers and collectors like Lower would see him as green and try to take advantage of him. But in general he regarded trade as honourable. He needed to get his insects out through the proper channels and did not see any of this as injurious to the pursuit of science. In sum, he was well above J. O. Westwood's definition of the very "lowest class of entomologists", a collector with inert drawers of "handsome insects".

Despite Dodd's many promises to Lyell, Kershaw and others that he would start to be more methodical in preserving dates and locations, as well as keep lists of his insects, he kept on failing to do so. As for keeping a collection of named specimens to guide him, this would not only be too cumbersome but also beyond what he could afford (National Museum of Victoria, 1 June 1911). It is difficult to determine if his shortcomings regarding taxonomic identification negatively affected his pricing. Although many of the letters contain lists with prices attached, we see him in his correspondence attempting to establish equivalencies and differences in value from one specimen to the next. Isolation, doubts about identification and the difficulty of knowing for certain if one's captures were rare were all inhibiting factors. The best he could do was to offer the insects in as perfect a condition as possible, along with close observation of their life histories. How did he classify himself? In the end, Dodd saw himself, not as an entomologist but as a professional collector, training up his four sons to be useful, all-round collectors across the various orders (National Museum of Victoria, 6 December 1912). One son, Alan Parkhurst Dodd (1896–1981), would in fact become a distinguished entomologist, collecting and importing live specimens of the *Cactoblastis* moth from Argentina to destroy the prickly pear that had spread over millions of acres of Queensland farmland. In Alan, F. P. Dodd's legacy lived on.

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Parasitoids of the uniquely social colletid bee *Amphylaeus morosus* (Hymenoptera: Colletidae) in Victoria

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Abstract

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Understanding how nest parasites contribute to brood mortality rates in host species is an important step towards uncovering the potential implications for host behaviour. This can be especially important for understanding the evolution of social living, where defence against parasites is often posited as a major benefit of cooperative nesting. Only two parasitoid species have previously been reported for the only known social colletid bee, *Amphylaeus morosus*: the gasteruptiid wasp, *Gasteruption primotarsale*, and the mutillid, *Ephutomorpha tyla*. Here we report six additional parasitoid species of *A. morosus*: the gasteruptiid wasps *G. atrinerve, G. globiceps, G. melanopoda* and *G. cinerescens*; the bombyliid fly *Anthrax maculatus*; and the mutillid wasp *Ephutomorpha* aff. *varipes*. The mechanisms of parasitism for these eight parasitoid species are described in combination with how they operate throughout the host brood rearing period and whether benefits of social nesting vary across the season.

Keywords

Bombyliidae, Gasteruptiidae, host-association, Hylaeinae, Mutillidae, parasitism

Introduction

Detailed host and parasite association data are important yet rarely explored for primitively social hosts, where defence against parasites is posited to be a driver of cooperative nesting. For insect parasitoids, the value of this information is often emphasised but is heavily weighted towards key taxon groups, such as Ichneumonidae, Braconidae, Chalcididae, Encyrtidae, Tachinidae and Bombyliidae, that are of economic importance (Heraty, 2017). Entomophagous insect associations with non-apid bees largely get overlooked but can have substantial consequences for brood mortality, behaviour and demography of host species (Segers et al., 2016; Smith et al., 2017). Additionally, parasite–host interactions in bees are seldom observed over their full life history, meaning the full series of parasites attacking a single host is often understated. In the small carpenter bees *Ceratina dupla* Say, 1837, and *C. calcarata* Robertson, 1900, Vickruck et al. (2010) reared a total of eight parasite species from brood cells after sampling nests across a six-month period. Wcislo et al. (2004) similarly sampled nests of the halictine bee *Megalopta genalis* (Meade-Waldo, 1916) across one year and reported four brood parasites infiltrating nests. However, Smith et al. (2017) noted that the full effect these brood parasites may have on the social nesting of *M. genalis* is hard to fully assess due to insufficient field data. For analogous species, the need for descriptive biological information combined with rigorous sampling across the colony life cycle is often needed to determine the true diversity and effect of brood parasitism.

The Australian hylaeine bee, *Amphylaeus morosus* (Smith, 1879) (Colletidae: Hylaeinae), is the only species in the hyper-diverse bee family Colletidae that is unambiguously known to exhibit social nesting. Social nesting in this species is very simple, with no known reproductive hierarchies or morphological differentiation between nestmates. *Amphylaeus morosus* has a semelparous and univoltine life cycle and may form social or solitary nests within the same population (Spessa et al., 2000). In the Dandenong Ranges, *A. morosus* uses naturally abscissed dead fronds of the rough fern tree *Cyathea australis* to construct linear nests out of the pithy interior. Like many hylaeine bees, *A. morosus* mass provision cells with a mixture of pollen and nectar before ovipositing into the cells.

Spessa et al. (2000) first reported a species of *Gasteruption* wasp, later identified as *Gasteruption primotarsale* Pasteels, 1957 (Gasteruptiidae) (Parslow et al.,

2020), attacking nests of *A. morosus* in the Dandenong Ranges, Victoria, while a species of mutillid wasp, *Ephutomorpha tyla* Hearn, Williams & Parslow, 2019 (Mutillidae), was recently reported entering nests late in the brood rearing season (Hearn et al., 2019). Spessa et al. (2000) found that social nesting in *A. morosus* seemed to provide only minimal benefits in reducing parasitism by *G. primotarsale*. However, that study did not consider possible defence benefits against other parasites, and indeed no other parasites were identified in that study. *Gasteruption primotarsale* parasitises the earliest brood during nesting period and may therefore only explain potential benefits of social nesting during the early stages of brood provisioning. Additionally, observations of *E. tyla* adults in the nest towards the end of brood-rearing (Hearn et al., 2019) suggest that *E. tyla* may exploit the mature larvae of *A. morosus* towards the end of its nesting period. It is important to understand the full suite of parasites that attack *A. morosus* because if these parasites operate at other times in the nesting period, that information will further our understanding of why social nesting in *A. morosus* persists until brood maturation. In south-eastern Queensland, Houston (1969) reported a range of parasites and parasitoids attacking *A. morosus* nests, including the wasps *Agamerion pulchra* (Pteromalidae: Cleonyminae), *Coelopencyrtus* spp. (Encyrtidae), *Gasteruption* sp. (Gasteruptiidae) and an acarid mite. However, in the Dandenong Ranges, little is known about the full range of parasites that might be involved.

Here, we identify eight different parasitoid species that attack *A. morosus*, including novel host records for the *Gasteruption* wasps *G. atrinerve* (Kieffer, 1911), *G. globiceps* Pasteels, 1957, *G. melanopoda* Pasteels, 1957, and *G. cinerescens* Schletterer, 1885, the bombyliid fly *Anthrax maculatus* Macquart, 1846 (Diptera: Bombyliidae), and the mutillid wasp *Ephutomorpha* aff. *varipes* (André, 1895). We examine the specific mechanisms of parasitism and eclosion timings of these parasitoids, which have been poorly understood. It is important that the respective host associations are well documented to fully recognise how these multiple parasitoid species may influence the nesting behaviour of the only known social bee in the colletid family.

Materials and methods

Nest collections

Nests of *Amphylaeus morosus* were collected from naturally abscissed fronds that haphazardly fall around the base of the rough tree fern *Cyathea australis* R.Br. Domin. These nests were collected in the Gembrook, Cockatoo and Marysville regions of the Dandenong Ranges, Victoria, Australia. Nests were sampled over five collection periods: 4–6 December 2017, 6–8 December 2018, 21–22 November 2019, 11 January 2020 and 27 February 2020. The collection region primarily consists of cool temperate montane habitat dominated by tall canopies of *Eucalyptus regnans* F. Muell and *E. viminalis* Labill, with a mixture of ferny, shrubby and grassy understories. Nests were collected early in the morning, late in the afternoon or during periods of light rain when bees were inactive to ensure all colony members were present. Nest entrances were sealed upon collection and all nests were stored in cool insulated boxes and transported to the laboratory where they were stored at 10°C until processed.

Parasitism data

Nests were dissected lengthwise and the contents, including adult female *A. morosus*, immatures and nest parasitoids, were recorded. Where possible, parasitised cells were carefully extracted from the nests and left to develop in Petri dishes at ambient room temperature. Petri dishes were kept moist by occasionally spraying filter paper rectangles inside each dish with water. Once the specimens had reached adulthood, defined as fully mature and mobile, they were placed in 99% ethanol for preservation and later identification. For parasitoids, where the pupal stages form cocoons (e.g. Mutillidae), at least one pupal case from each nest was dissected in coordination with the nest being opened to determine the developmental stage of each immature.

Not all the *Gasteruption* specimens were successfully reared to pupae or adulthood because developmental rates for *Gasteruption* species lagged significantly behind host maturation rates; due to this, the specific parasitisation rates for each *Gasteruption* species were unable to be determined. Further, the scarcity of larval descriptions based on morphology for the genus *Gasteruption* made it impossible to discriminate species at the larval stage (Bogusch et al., 2018). Therefore, the parasitisation rates for each species are combined and treated at the genus level *Gasteruption*.

Specimen identification

Specimens were examined using a Nikon SMZ1000 stereomicroscope at the South Australian Museum, Adelaide, Australia. Images were taken using a Visionary Digital LK imaging system (Dun, Inc.) with a Canon EOS 5DsR camera at Flinders University, Adelaide, Australia. Images were produced using Zerene Stacker (Zerene Systems LLC) software and cropped and resized in Photoshop CS5.

Material examined in this study were initially identified using the following keys: *Amphylaeus morosus* specimens were identified using Houston's (1975) key to Australian hylaeine bees; *Gasteruption atrinerve*, *G. globiceps*, *G. melanopoda*, *G. primotarsale* and *G. cinerescens* were identified by B.A. Parslow (South Australian Museum) using Pasteel's (1957) key to the Australian *Gasteruption* and comparison with type material; *Ephutomorpha tyla* specimens were identified by L.R. Hearn by comparing specimens with type material held at the South Australian Museum; and *Anthrax maculatus* was identified by X. Li (Florida Museum). Voucher specimens for the examined species have been deposited at the Melbourne Museum (Table S1).

DNA sequencing for the eight parasitoids of *A. morosus* was performed by the Canadian Centre for DNA Barcoding at the Biodiversity Institute of Ontario using standard protocols (Ivanova et al., 2006; Table S1).

Table 1. Prevalence of parasitoid species in host nests and brood cells at each collection period. Mean parasitised cells calculated from parasitised nests only*.

Nest collection			Parasitised nests				Parasitised cells (total/mean)*			
Year	Total nests	Total cells	*Gasteruption*	*Anthrax maculatus*	*Ephutomorpha tyla*	*Ephutomorpha* aff. *varipes*	*Gasteruption*	*Anthrax maculatus*	*Ephutomorpha tyla*	*Ephutomorpha* aff. *varipes*
Early summer 2017	85	400	16	0	9	0	22/1.38	0/0	37/4.11	0/0
Early summer 2018	6	29	0	2	0	0	0/0	7/3.5	0/0	0/0
Late spring 2019	27	124	7	0	0	0	9/1.29	0/0	0/0	0/0
Mid-summer 2020	26	109	1	2	2	1	1/1	15/7.5	4/2	8/8
Late summer 2020	16	78	3	0	4	0	3/1	0/0	26/6.5	0/0
Total	**160**	**740**	**27**	**4**	**15**	**1**	**35/1.29**	**22/5.5**	**67/4.47**	**8/8**

Results

Nest architecture and composition

In the Dandenong Ranges, females of *A. morosus* construct their nests in dead abscissed fronds of the rough fern tree *Cyathea australis* by excavating the pithy interiors of the stems to create an unbranched linear tunnel. Nests were on average 212.63 ± 59.39 mm long (mean ± standard deviation; $N = 156$) with nest entrance diameters of 5.65 ± 0.61 mm ($N = 52$). In other regions, nests also occur in the dead flower scapes of *Xanthorrhoea* spp. (L. Hearn, personal observation). The tunnel is lined with a cellophane-like material, a characteristic common to hylaeine bees, that is thought to act as a waterproofing and antimicrobial agent (Almeida, 2008). Provisioning of brood cells generally begins in mid-spring, and cells are laid sequentially starting from the distal end of the fern frond towards the proximal end. Brood production can last until mid-summer across the Dandenong Ranges populations, allowing different parasitoid species to attack at different brood development stages (fig. 1).

Nest architecture in *A. morosus* can be broadly categorised into nests with brood cells interspersed with vestibules and nests with brood cells laid sequentially (fig. 2). Vestibules are empty spaces containing no provisions or brood and are common in many stem-nesting Hymenoptera (Danks, 1971). In *A. morosus,* vestibular cells are frequently found in solitary nests, but nest burrows are fully excavated before the first cell is provisioned. This limitation to nest length once cell provisioning has begun suggests that there may be a trade-off between the number of potential brood cells and constructing vestibular cells to deter nest parasitoids.

Host associations

***Gasteruption* Latreille, 1796 (fig. 3a).** *Gasteruption* is the most abundant parasitoid of *A. morosus* in terms of nests parasitised, parasitising 16.9% (27/160) nests across all collection periods (Table 1). Of the nests parasitised by *Gasteruption*, only the first three brood cells were found to contain parasitoid immatures. *Gasteruption* parasitised cells were often followed by vestibular cells (11/35 parasitised cells), detritus (9/35) or provisioned cells that failed to develop (4/35).

The larvae of *Gasteruption* are predator-inquilines in the nests of *A. morosus* where they kill the host egg or developing host larva before consuming the entire host provisions (Bogusch et al., 2018; Parslow et al., 2020). They then construct, using anal secretions, dark semi-cocoons above and below the larvae separating the parasitised cell from the rest of the nest (Eardley and Daly, 2007; Malyshev, 1968; Westrich, 2018). Although some species of *Gasteruption* have been reported to consume the contents of multiple adjacent cells (Donovan, 2007; Malyshev, 1968; Westrich, 2018), *Gasteruption* immatures were only observed to occupy a single host cell in our nests of *A. morosus*.

Adult eclosion of *Gasteruption* occurred far later in the season compared with *A. morosus* (fig. 4). In most cases, *Gasteruption* brood were still at a late larval stage at the time *A. morosus* cells were reaching adult eclosion. Five species of *Gasteruption* were reared from host nests. One of these, *Gasteruption primotarsale* Pasteels, 1957, has been previously recorded from nests of *A. morosus* (Spessa et al., 2000). The novel host association for *G. atrinerve* (Kieffer, 1911); *G. globiceps* Pasteels, 1957; *G. melanopoda* Pasteels, 1957; and *G. cinerescens* Schletterer, 1885, were determined using adults reared from host nests.

***Anthrax maculatus* Macquart, 1846 (fig. 3d).** Four nests were found to be parasitised by the bombyliid fly *Anthrax maculatus* across two separate sampling periods. *Anthrax maculatus* was never directly observed ovipositing into or hovering around the nests of *A. morosus*. Yet, developing *A. maculatus* immatures were found occupying both single and consecutive *A. morosus* brood cells, accounting for 24.1% (7/29) and 13.8% (15/109) of the total brood cells across the early summer (December 2018) and mid-summer (January 2020) collection periods, respectively. The pupae of *A. maculatus* were primarily observed occupying cells in the middle of the nests, but in one instance, every cell in the nest contained parasitised immatures. All brood cells parasitised by *A. maculatus* contained late-stage pupae when the nest was opened, and in nests containing both *A. maculatus*

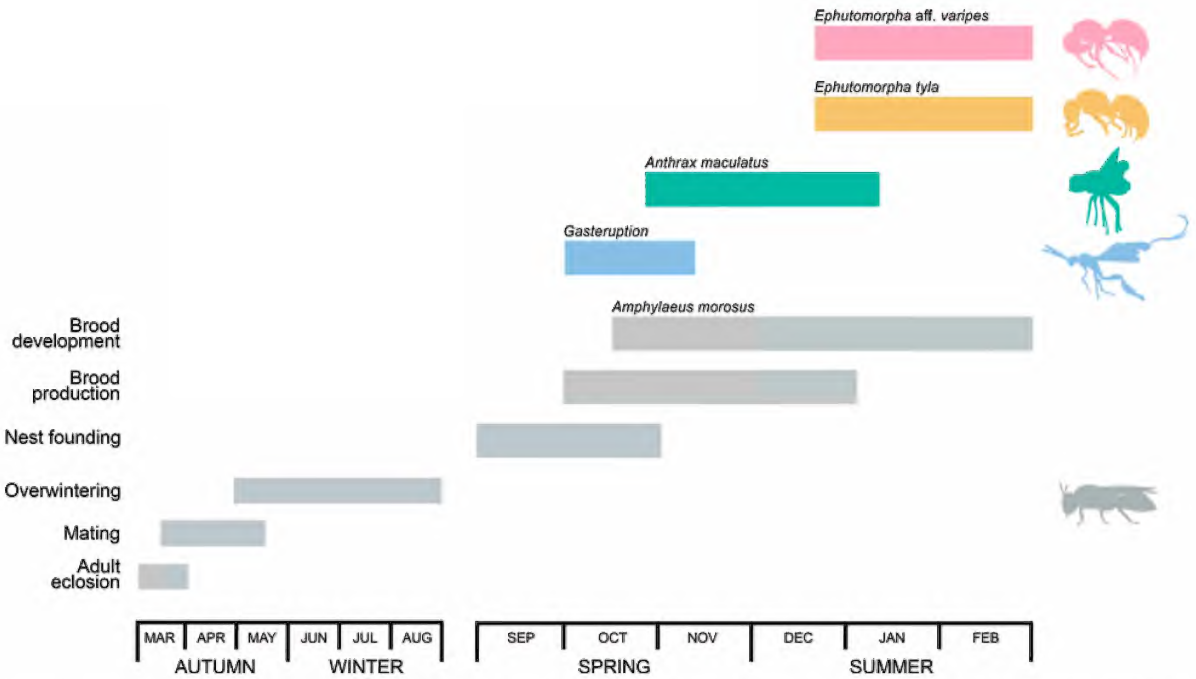

Figure 1. Annual cycle of *Amphylaeus morosus* across the full univoltine, semelparous life cycle in the Dandenong Ranges, Victoria (grey). The timings of nest parasite attacks (coloured) were estimated from rates of occurrence in nests across the brood development period.

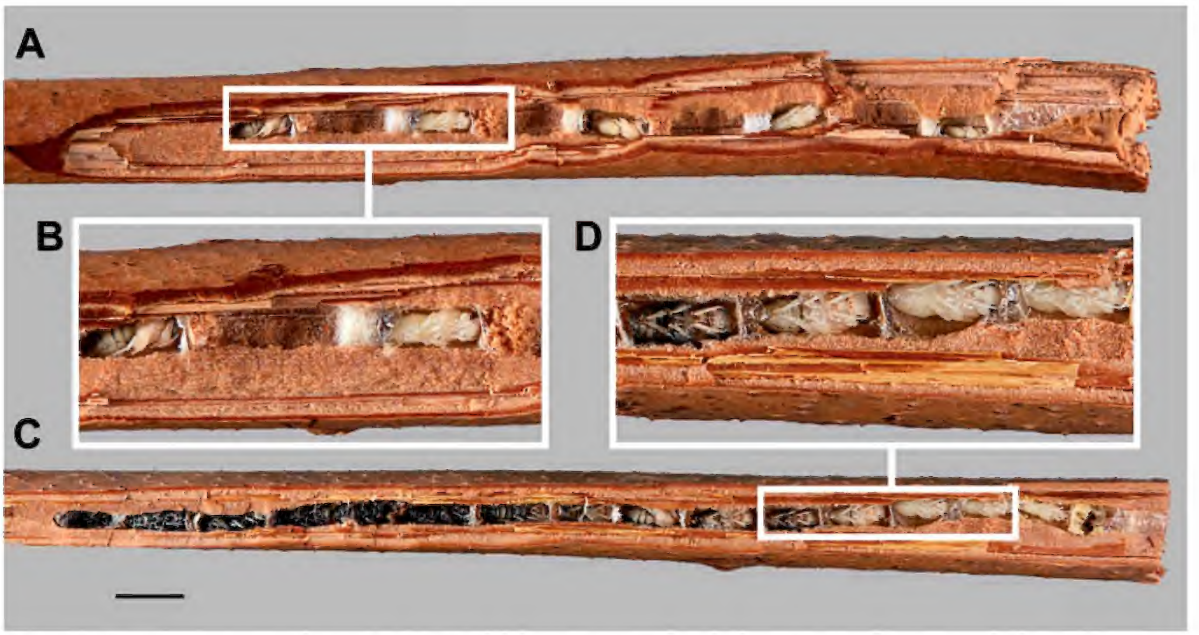

Figure 2. Nest dissections showing the two typical nesting structures for *Amphylaeus morosus* in the Dandenong Ranges: a, typical structure of a solitary nest; b, close-up of brood cells directly followed by a pithy cell plug, interspersed with vestibular cells; c, typical structure of a social nest; d, close-up of brood cells laid sequentially. Scale bar = 10 mm.

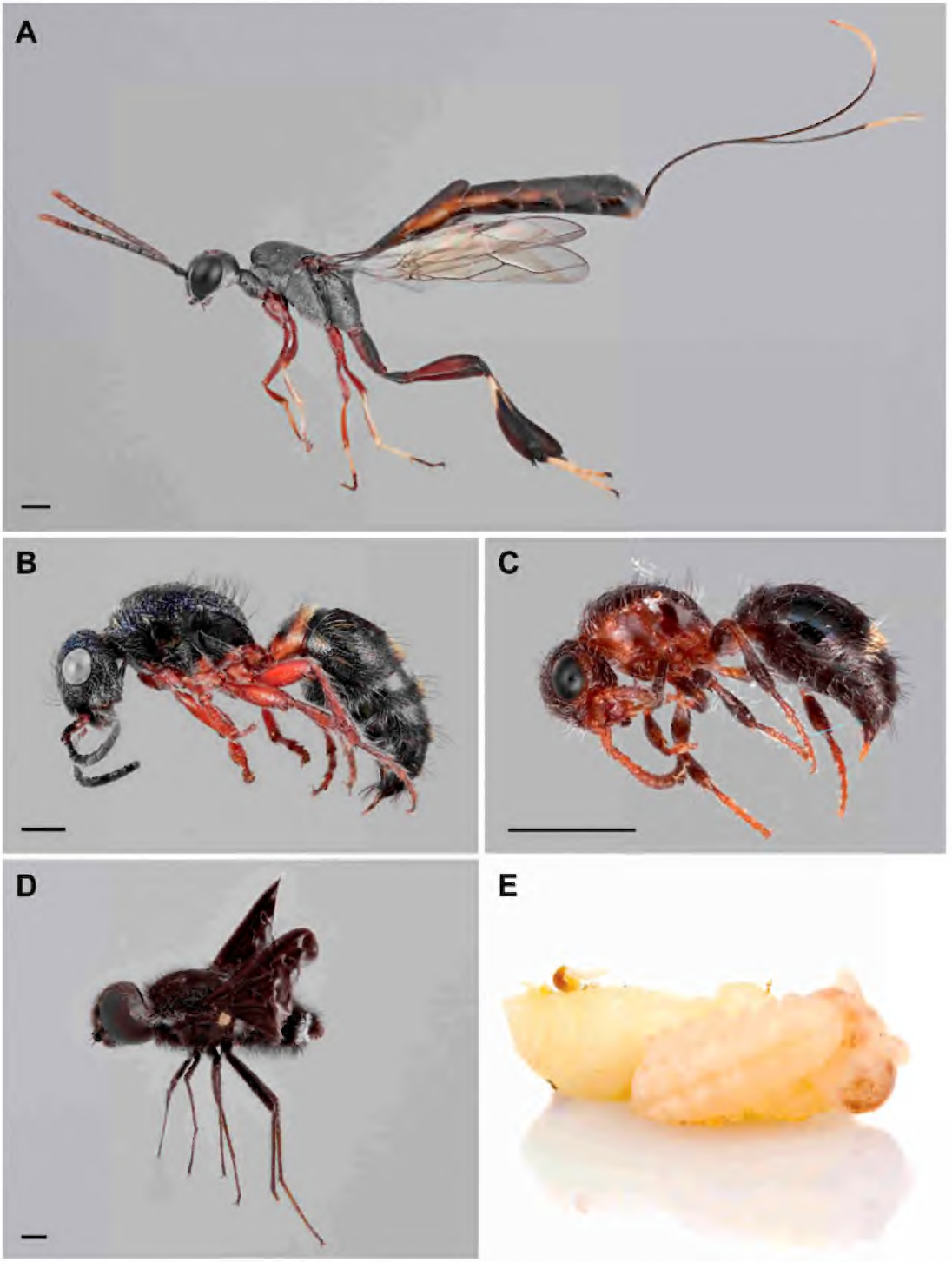

Figure 3. Images of the parasitoids reared from *Amphylaeus morosus* nests: a, lateral habitus of *Gasteruption globiceps*; b, lateral habitus of *Ephutomorpha tyla*; c, lateral habitus of *Ephutomorpha* aff. *Varipes*; d, lateral habitus of Anthrax maculatus e, *Ephutomorpha* aff. *varipes* larvae feeding on *A. morosus* pupae (photo credit James Dorey, 2020). Scale bar = 1.0 mm.

immatures and unparasitised host immatures, the host brood cells contained mid- to late-stage pupae. The pupae of *A. maculatus* were packed into the host brood cells and eclosed to adults within minutes of being extracted from the brood cell in the nest. The emergence of adult *A. maculatus* therefore appeared to be stimulated by disturbance but still synchronised with host adult eclosion (fig. 4).

***Ephutomorpha tyla* Hearn, Williams, and Parslow, 2019 (fig. 3b).** The host association for *Ephutomorpha tyla* has already been described by Hearn et al. (2019). Here, we present additional details based on new data. In two nests, a single adult female *E. tyla* was observed trying to break through the most proximal cell in the nest, while in a further 21 instances, adult females were observed waiting in the nest entrance. *Ephutomorpha tyla* does not appear to specifically target certain nest types, attacking nests with up to 14 brood cells or nests with only four brood cells interspersed with vestibules. A total of 29 nests contained either parasitised immatures, an adult female *E. tyla* in the entrance, or both. No adult female *A. morosus* were present in 69% (20/29) of these nests.

Parasitised brood cells consisted of brown papery cocoons that occupied the entirety of the brood cell. As the *E. tyla* immatures developed, the brood cells became darker and increasingly difficult to open. In nine affected nests, all brood cells were parasitised by *E. tyla*, with damaged partitions between cells. The body sizes of male and female *E. tyla* were generally consistent. However, in some cases there were marked differences in body size within each sex.

***Ephutomorpha* aff. *varipes* (André, 1895) (fig. 3c).** Larvae of *Ephutomorpha* aff. *varipes* were observed as external parasitoids of the mature larvae, prepupae and pupae of *A. morosus* and were observed feeding on young pupae (fig. 3e). Larvae of *E.* aff. *varipes* remained on their host until mature before producing a light-brown silk-like cocoon and eclosing as an adult. The ectoparasitoid larva of *E.* aff. *varipes* were observed on multiple consecutive *A. morosus* immatures in one nest. The first three brood cells of the parasitised nest contained fully healthy *A. morosus* immatures, whereas the next eight brood cells were occupied by parasitised larvae, all of which eclosed as males. *Ephutomorpha* aff. *varipes* was observed

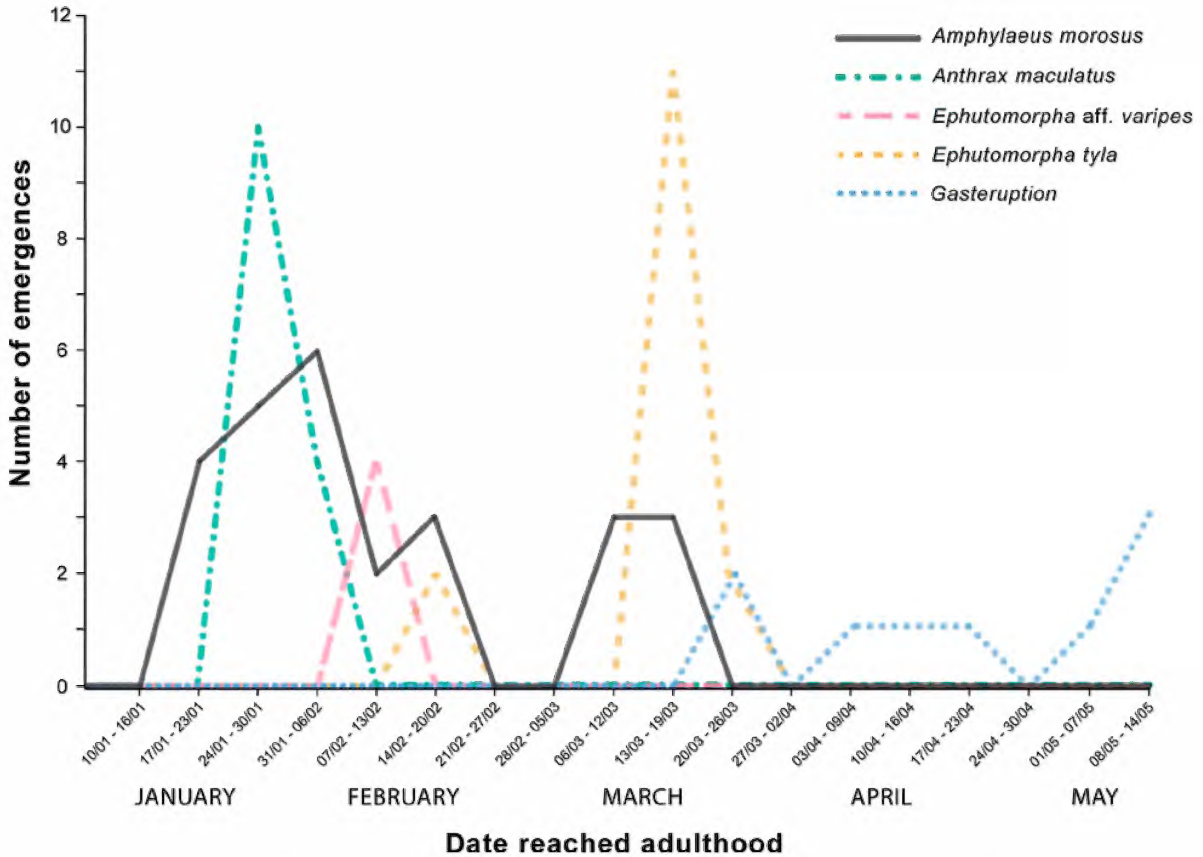

Figure 4. Eclosion phenologies of *Amphylaeus morosus* and its nest parasites. Emergence observations are only reported for the provisioning and rearing phase during 2019. Host emergences are only reported for nests containing parasitised brood.

parasitising several species that occupy excised *Cyathea australis* fronds, including another mass provisioning bee, *Hylaeus* sp., and a crabronid wasp, *Pison* sp. While, on numerous occasions, females were observed in the nest entrance of the allodapine bee, *Exoneura robusta* Cockrell, 1922, no parasitic association has been confirmed.

Other enemies

Of the 243 potentially viable *A. morosus* nests collected, 34.2% (83/243) contained no *A. morosus* adults or brood cells and had been superseded or temporarily occupied by other insect species. Twenty-four of these nests were occupied by *Pison* sp. (Hymenoptera: Crabronidae), two nests were occupied by the pteromalid wasp of the genus *Eupelmophotismus* (Hymenoptera: Pteromalidae), while one nest contained recently eclosed encyrtid wasps from the genus *Coelopencyrtus* (Hymenoptera: Encyrtidae). Five nests contained clerid beetle larvae (Coleoptera: Cleridae), including two instances of nests with *A. morosus* immatures and adults that contained beetle larvae in the nest entrance.

Discussion

Nest parasitoids are known to have detrimental effects on the survival and productivity of bees (Vickruck et al., 2010; Wcislo et al., 1994). Of the parasitoid species that attack *A. morosus*, the predator-inquilines of the genus *Gasteruption* were the most prevalent, but least detrimental, only parasitising a mean of 1.29 cells per infiltrated nest, with 16.9% of nests being infiltrated. We never observed *Gasteruption* entering nests of *A. morosus*, possibly because our nest collections were restricted to cool weather conditions when insect activity was low; it is likely that *Gasteruption* wait for the adult bee to leave before infiltrating the nest and ovipositing in an open brood cell (Macedo et al., 2012; Parslow et al., 2020). Parasitisation by *Gasteruption* was only observed in single female nests, which suggests that multifemale nests are guarded by one female while other individuals collect provisions, restricting the opportunity for wasps to oviposit (Parslow et al., 2020). The extended development time of *Gasteruption* in *A. morosus* nests has been similarly reported in *Gasteruption brachychaetum* Schrottky, 1906a, larvae in nests of *Hylaeus* aff. *guaraniticus* (Schrottky, 1906b) (Macedo et al., 2012). The resulting asynchrony in adult emergence between *Gasteruption* immatures and host could be attributed to delaying their eclosion until hosts have started establishing new nests, which may explain observations of *Gasteruption* pupae in overwintering *A. morosus* nests (L. Hearn, personal observation). For *Gasteruption*, parasitising the distal nest cells could be a factor of this extended development period and avoiding being disturbed by emerging bees and other emerging parasitoids. There is limited information on *Gasteruption* host specialisation, with a large proportion of records based on single observations (Parslow et. al. 2020). It is unlikely that *A. morosus* is the only host for *G. atrinerve*, *G. globiceps*, *G. melanopoda* and *G. cinerescens* because their distributions extend beyond the distribution of *A. morosus* (Atlas of Living Australia 2021; Parslow, 2020; Pasteels, 1957).

In contrast, parasitisation by the dipteran *Anthrax maculatus* had a greater effect when invading *A. morosus* nests, parasitising 5.5 brood cells on average across *A. maculatus* infiltrated nests. Previous studies have suggested that adult bombyliid females identify a host nest and oviposit directly into the nest entrance (Bohart et al., 1960). However, there are also reports of adults ovipositing haphazardly onto the ground, leaving the planidium to search for a host nest (Yeates and Greathead, 2008). This latter scenario could be likely in the Dandenong Ranges given the high density of *A. morosus* nests that can occur. It was unknown if the larvae of *A. maculatus* feed on both the immatures and provisions in a cell. Gerling and Hermann (1976) reported early instar larvae of the bombyliid fly, *Xenox tigrinus* (Evenhuis, 1984) (previously *Anthrax tigrinus*), feeding on the pollen bread in *Xylocopa virginica* (Linnaeus, 1771) nests. However, bombyliid fly immatures are also known to feed on the mature larvae of their hosts (Felicioli et al., 2017; Minckley, 1989). The delay in adult eclosion by *A. maculatus* compared with its host is consistent with observations by Minckley (1989) of *Anthrax xylocopae* (Marston, 1970) delaying emergence to synchronise with its host. This is because adults are not able to break through the cell partitions and therefore must wait for hosts to emerge (Gerling and Hermann, 1976). This could explain why *A. maculatus* puparium in our current study appeared to be stimulated by disturbance when removed from their cells.

In our study, *Ephutomorpha tyla* was the most abundant and destructive nest parasitoid in terms of both the number of brood cells parasitised and (potentially) adult hosts killed. *Ephutomorpha tyla* was rarely observed in nests with an adult host present, supporting similar reports of mutillids forcefully removing or killing host guards before ovipositing (Brothers et al., 2000). Adult *E. tyla* were generally observed in the nest entrances and on some occasions attempting to break through the cell closest to the entrance, suggesting that *E. tyla* may open the brood cell closest to the entrance to check for host brood before ovipositing. The size differences between reared adults of *E. tyla* are likely due to differences in the consumed host immatures. For instance, in *A. morosus*, the males are generally smaller than the females (Spessa, 1999). Additionally, the amount of provisions in each brood cell can vary dramatically, which can influence the size of the host immatures and subsequently the ectoparasitoid feeding on it (Brothers, 1989). Comparatively, the size differences observed in adults of *E.* aff. *varipes* support the notion that it is likely a parasitoid of multiple insect hosts; this accords with reports by Mickel (1928) that variation in body sizes within mutillid species is linked to them exploiting a range of hosts of varying size. *Ephutomorpha* aff. *varipes* was observed in nests of numerous different host species including the allodapine bee, *Exoneura robusta* Cockerell, 1922. However, given Brothers' Rule (Brothers et al., 2000), which states mutillids will only attack fully enclosed immatures, it is unlikely that such a condition is universal given that *E. robusta* progressively rears its brood in open linear nests. These observations suggest that *E.* aff. *varipes* is a generalist parasitoid of hosts using *Cyathea australis* as a nesting substrate, rather than any specific hymenopteran host, which accords with the notion that some mutillid species are adapted to specific situations rather than hosts (Brothers, 1989).

Attack by wingless parasitoids such as mutillid wasps is uncommon in stem-nesting bees (Ronchetti and Polidori, 2020). Michener (1985) suggested that this may be because predators need to search in a three-dimensional space looking for sparsely distributed nesting sites, whereas ground-nesting hymenopteran entrances can be found using a two-dimensional search pattern. In *A. morosus*, the high rates of parasitism might be attributable to the high density of their nesting substrate around mature tree ferns (Groulx and Forrest, 2018). This high density of nesting sites may act in a similar system to the ground nesting aggregations of halictid bees, where nesting sites are abundant, and parasitism can be prevalent (Wcislo, 1996).

The mechanisms of parasitism and bionomy of parasitoids has generally been poorly understood. Our study finds that parasitoids of *A. morosus* have adapted to host nesting behaviour and suggests variation in the oviposition chronology of each parasitoid species, with *Gasteruption* wasps ovipositing at the beginning of brood provisioning, *A. maculatus* ovipositing across the middle stages of brood development and the two mutillid species ovipositing in nests at the end of the season. This variation in parasitoid pressure could have implications for understanding the factors driving social nesting in the only known social bee in the family Colletidae.

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Supplementary material

Table S1. Table showing BOLD sequencing reference number and voucher number for deposited material. All material deposited at Melbourne Museum.

Family	Species	Melbourne Museum Voucher number	BOLD reference number
Gasteruptiidae	*Gasteruption primotarsale*	HYM-97074	OZBOL2593-21
Gasteruptiidae	*Gasteruption globiceps*	HYM-97075	OZBOL2607-21
Gasteruptiidae	*Gasteruption atrinerve*	HYM-97076	OZBOL2606-21
Gasteruptiidae	*Gasteruption cinerescens*	HYM-97077	OZBOL2605-21
Gasteruptiidae	*Gasteruption melanopoda*	HYM-97078	N/A
Bombyliidae	*Anthrax maculatus*	DIP-2590	OZBOL2594-21
Mutillidae	*Ephutomorpha tyla*	HYM-97079	OZBOL2596-21
Mutillidae	*Ephutomorpha* aff. *varipes*	HYM-97080	OZBOL2599-21

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Early land plants from the Lower Devonian of central Victoria, Australia, including a new species of *Salopella*

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Abstract

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Early land plants with elongate sporangia held in the palaeobotanical archives of Museums Victoria were examined. The fossil plants are from Yea (?upper Silurian) and near Matlock (Lower Devonian) in central Victoria, and are of interest because they contribute to our understanding of the evolution of early land plants in a region in which research has been limited. Both *Salopella australis* and *Salopella caespitosa* were originally described over 30 years ago and this reinvestigation has resulted in the emending of the diagnosis of *Salopella australis* and the erection of a new morphotaxon *Salopella laidae* sp. nov. based primarily on differing branching architecture and sporangial morphology. *Salopella laidae* comes from Yea Formation and possesses regular isotomous branching over at least two orders of branching, terminating in elongate sporangia that are wider than their subtending axes, differing from *S. australis,* which possesses only one dichotomy emanating from at least two erect parallel parent axes with sporangia that are the same width as their subtending axes. A recently collected specimen of *Salopella caespitosa* was also examined and adds to our understanding of this taxon, which was previously only known from one specimen. Consideration is given to the possible sources of these early land plants based on other early land plants with a similar grade of organisation.

Keywords

embryophytes, rhyniophytoids, *Baragwanathia* flora, Devonian, Victoria

Introduction

Fossil plants have been known in Victoria since the 19th century (Nicholas, 1875). Palaeobotanical studies on the *Baragwanathia* flora (Jaeger, 1966) from the Silurio-Devonian of Australia have primarily been limited to the first half of the twentieth century (Cookson 1935, 1937, 1949; Lang and Cookson, 1927, 1930, 1935) and further expanded with Tims (1980), Tims and Chambers (1984) and McSweeney et al. (2020). The majority of plant fossils have been uncovered in the Melbourne Zone (fig. 1), and some further fragmentary remains have been found further south in the Mathinnia Group of northeastern Tasmania (Baillie et al., 1989; Banks, 1962; Cookson, 1937; Powell et al., 1993). New data on early land plants from Australia, which was once part of northeastern Gondwana during the Silurio–Devonian periods, is of significance globally because it allows comparisons between floral assemblages in Laurussia (Europe, the United States and Canada), mid-palaeolatitude (Argentina) and high palaeolatitude (Bolivia and Brazil) western Gondwana sites and Chinese sites (North and South China Plates; Torsvik and Cocks, 2019). Furthermore, the new data allow for more data to be acrued to test the hypothesis of a Lower Devonian northeastern Gondwana phytogeographic unit within which both South China and Australia were parts or subunits of, according to Hao and Gensel (1995, 1998, 2001) and Wang et al. (2002).

This paper records one new taxon after an investigation of early land plant material with elongate sporangia collected by Tims and Chambers (1984) from the ?upper Silurian–Lower Devonian Yea Formation, the Humevale Formation near Yea and the Lower Devonian Wilson Creek Shale Formation near Matlock in central Victoria (fig. 1). Early land plants possessing elongate sporangia with tapering apices of either rounded or pointed tips and with fusiform or elongate parallel sided sporangia characteristic of rhyniophytes/rhyniophytoids (*sensu* Edwards & Edwards 1986) were described by Tims and Chambers (1984) and assigned to *Salopella australis* and *Salopella caespitosa*. The specimens described herein are compressions/impressions with little anatomical detail preserved and belong to the same morphogenus *Salopella* Edwards and Richardson, 1974. One new specimen of *S. caespitosa,* only the second so far recorded, was also

examined and is of siginifcance to our understanding of this morphotaxon because it was preserved in semi-relief as a coalified compression/impression.

Locality, stratigraphy and age

The Melbourne Zone is a triangular stuctural region occuping central Victoria bounded by the Heathcote Fault in the west and Governor Fault in the east, opening towards the south (VandenBerg and Gray, 1988). The Wilson Creek Shale extends across the Melbourne Zone (VandenBerg, 1975; VandenBerg et al., 2006), and based on the conodont fauna, is considered to be middle Pragian–Emsian (Mawson and Talent, 1994). It comprises mudstone and shale units, characteristic of deep water and anoxic conditions, with *Uncinatograptus thomasi* (=*Monograptus thomasi*) Jaeger, 1966, found throughout and *Neomonograptus notoaequabilis* (=*Monograptus aequabilis notoaequabilis*) Jaeger et al., 1969, in the upper half (Edwards et al., 1997, 1998; Lenz 2013; VandenBerg, 1988; VandenBerg et al., 2006). The outcrop examined occurs on Frenchmans Spur track, approximately 10 km west of Matlock, and is the type location of the rhyniophytoids *Salopella australis* and *S. caespitosa*, and the early "trimerophyte-grade" (*sensu lato* Banks 1975) plant *Dawsonites subarcuatus* (Tims and Chambers, 1984).

The Humevale Siltstone and Yea Formation occur in the western part of the Melbourne Zone (Edwards et al., 1997; VandenBerg, 1988) and both are exposed near Yea. The dating of the exposures at Ghin Ghin Road and Limestone Road, Yea, as Pridolian and Ludlovian respectively by Garratt and Rickards (1984, 1987), Garratt et al. (1984), Rickards and Garratt (1990), and Rickards (2000) are contentious for a number of workers (Banks 1980; Cleal and Thomas, 1999;

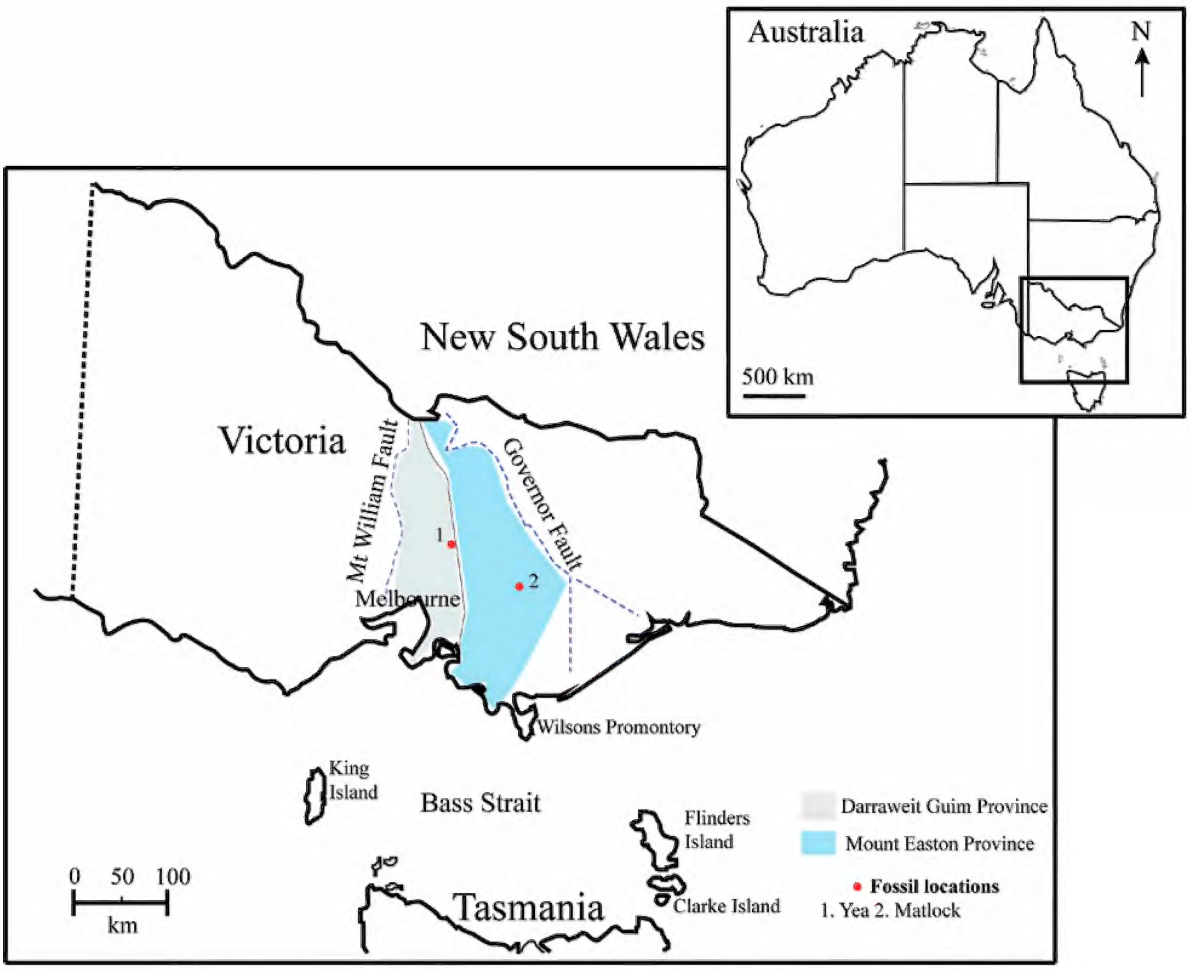

Figure 1. Map of Victoria, Australia, showing the fossil locations within the Melbourne Zone. Location 1. Yea, Ghin Ghin Road, Limestone Road (37° 12.38' S, 145° 25.39' E). Location 2. Matlock, Frenchmans Spur (37° 25.82' S, 146° 77.24' E.), the type location of *Salopella australis* and *S. caespitosa* (Tims and Chambers, 1984). Source: adapted from Moore et al. (1998: fig. 2).

Edwards et al., 1979; Edwards et al., 1997; Hao and Gensel, 2001; Hueber, 1983, 1992). Hueber (1983) considered the morphological and anatomical complexity of *Baragwanathia longifolia* more akin to a Lower to Middle Devonian age and noted the complex nature of the conspecific taxa *Yarravia (=Hedeia)* to further that point, McSweeney et al. (2021). Hueber (1992) suggested differences between the *Baragwanathia* from the two horizons at Yea were likely intraspecific and considered the interpretation of graptolites by Garratt and Rickards (1984) as subjective because preservation was poor. Additionally, Hueber (1992) highlighted that the purported 24 million year difference between the two horizons had resulted in little evolutionary change, as did Hao and Gensel (2001: 103), yet massive differences occurred over 3 million years between the *Cooksonia* spp. found in Ireland (Edwards et al., 1983) and the younger Lower Plant Horizon of Yea. Edwards et al. (1979: 321) questioned the interpretation of the age of *Maoristrophia banksi* and the graptolites not occurring on the same plane as the *Baragwanathia* in the Lower Plant Horizon. Finally, Edwards et al. (1997: 22) consider the Humevale and Yea Formations at Yea to be part of the Norton Gully Sandstone Formation.

The Yea and Humevale Formations espoused by Garratt (1978) are retained because they provide a stratigraphic framework for the area (McSweeney et al., 2020: fig. 2 – stratigraphical comparison chart and Ghin Ghin Road exposure). However, a Lower Devonian age will be used when assigning an age to specimens at Yea to account for these differing interpretations.

Materials and methods

The collection site of early land plants from Limestone Road, Yea, is heritage listed, with further collecting forbidden; in addition, the Frenchmans Spur locality is heavily overgrown and, for the most part, inaccessible. The specimens described herein are from Museum Victoria's palaeontological archives and were collected by J.D. Tims and J. Douglas in the 1970s and early 1980s, and one specimen *S. caespitosa* (NMV P235941) collected by C. Earp and M. Pepper, 19 m from the Devil's Elbow road cutting on Ghin Ghin Road, Yea, central Victoria, Australia.

The specimens collected by Tims and Douglas are preserved as fine compressions/impressions, and even after maceration with Schultze's solution and acetate film pulls (see Tims and Chambers, 1984: 266), no evidence of internal anatomy remains. The *S. caespitosa* collected by Earp and Pepper is coalified and a fragment was taken from the lowest part of the parent axis of NMV P235941.2 using a fine steel needle. Additionally, a fragment was dislodged from the centre of the basal dark presumed sporogenous region of sporangia two and four on NMV P235941.1. These fragments were placed onto aluminium stubs for scanning electron microscope analysis under low vacuum on an FEI Quanta 200 ESEM at RMIT University's RMIT Microscopy and Microanalysis Facility (RMMF).

Images were taken at Museums Victoria (Carlton) using a Leica M205 C microscope and Leica Application Suite software version 3.8.0. Images were edited using Adobe Illustrator CC 2017 and morphological measurements were taken using ImageJ software. Dégagement was undertaken on the Museums Victoria material archived by Tims (1974, 1980), Tims and Chambers (1984) and J. Douglas.

Institutional abbreviations

NMV P, Museum Victoria Palaeontology Collection, Melbourne, Australia. The use of .1 and .2 at the end of NMV P refer to part and counterpart, respectively. All specimens including the samples placed on stubs for scanning electron microscope analysis are housed in the Palaeontological Section, Museums Victoria, Melbourne.

Systematic palaeobotany

Plantae. *Incertae sedis*

Genus. *Salopella* Edwards and Richardson, 1974

Type Species. *Salopella allenii* Edwards and Richardson, 1974

Salopella australis Tims and Chambers, 1984 (fig. 2A–G; line-drawing fig. 6A)

Salopella australis Tims and Chambers (1984: pl. 32, figs. 1–6; pl. 34, figs. 4, 5; text-fig. 2A–C)

Emended diagnosis (after Tims and Chambers, 1984). New information in bold. Axes 0.9–2.4 mm wide with central line, **at least two long aligned parallel parent axes** with **one dichotomy each resulting in narrower shorter daughter axes terminated by a single sporangium on each.** Plant at least **80 mm high**. No obvious branching at the base of the sporangia. Sporangia 6.5–14.0 mm high and 1.3–2.0 mm wide, with parallel sides in the lower two-thirds of the presumed fertile portion. Sterile sporangia apex tapering to a point in the upper third. Spore characters unknown.

Locality. Frenchmans Spur Track, 10 km west of Matlock, Victoria. 37° 25.82' S, 146° 77.24' E.

Stratigraphy and age. Wilson Creek Shale, mid-Pragian–Emsian, Lower Devonian (Carey and Bolger, 1995; Mawson and Talent, 1994).

Note: Two specimens assigned to *S. australis* by Tims and Chambers (1984) from Limestone Road have been transferred to Gen. et sp. indet. because the specimens are too poorly preserved to unequivocally assign to any taxon. These are NMV P229617 and NMV P157323; NMV P157323 (Jack Douglas Private Collection) was figured by Tims and Chambers (1984: pl. 32, figs 5, 6 and text-fig. 2b) but possesses a completely different branching architecture to the holotype for *S. australis* and has poorly defined sporangia. Specimen NMV P157323 has been re-drawn here (fig. 6B) for comparison to *S. australis* (fig. 2A–E). Specimen NMV P50011 from Limestone Road has been moved out of *S. australis* to a new *Salopella* species (see below). Most specimens assigned to the Wilson Creek Shale by Tims and Chambers (1984) on Frenchmans Spur track are considered *S. australis* because they have subtending axes the same width

as their sporangia (e.g. NMV P50014, NMV P33219 and NMV P50008 [holotype]). Only in cases where this character is equivocal are specimens assigned to Gen. et sp. nov. (e.g. NMV P50010).

Description. *Salopella australis* possessed an erect habit with at least two long parent axes aligned parallel to each other and with one distal dichotomy on each resulting in narrower shorter daughter axes, each terminating in an elongate sporangium with an acuminate apex. A slight indentation occurs on some sporangia at the darker carbonaceous area and sterile interface, and proximally the dark carbonaceous area tapers inwards on the daughter axes.

Remarks. A reassessment of the morphospecies *Salopella australis* as originally determined by Tims and Chambers (1984) has necessitated the removal of some of the specimens attributable to it, primarily due to differing branching architectures and poor preservation. Tims and Chambers (1984: 268) noted four species with two dichotomies, but only three were found; presumably, the fourth is in a private collection. Nonetheless, all the specimens figured in Tims and Chambers (1984) were examined. Tims and Chambers (1984: 270) described *S. australis* as "open-branched" (Tims and Chambers, 1984: pl. 32, fig. 5, 6) with at least two dichotomies of widely dichotomising daughter axes emanating from one parent axis, and up to at least 145 mm in length (fig. 6B). However, this was found to occur on only three specimens from Limestone Road and was not found on the holotype (fig. 2D, E – double arrows between aligned parent axes).

The holotype possessed two aligned parent axes, with one of the parent axes dichotomising into shorter narrower daughter axes. The other parent axis was not as well preserved. However, another specimen with better preservation (fig. 2A, C) shows both parent axes aligned and dichotomising into shorter narrower daughter axes terminated with elongate sporangia that are no wider than their subtending axes. Tims and Chambers (1984: pl. 32, fig. 4) partly illustrated this specimen with only one of the parent axes shown. However, Tims and Chambers (1984) did not mention or show the other parent axis aligned parallel to this axis. Furthermore, there was an additional specimen in the collection not figured by Tims and Chambers (1984), likely due to its poor preservation, but which also had two aligned almost parallel axes and is similar to the holotype with two parent axes aligned and with one of the parent axes possessing a single dichotomy with short daughter axes terminated in elongate sporangia (fig. 2B). Even taking into account the effects of degradation of the specimens before fossilisation and the effects of ocean currents on orientation of the axes, the Limestone Road specimens appears to have more in common with *S. caespitosa* than *S. australis*, with two dichotomies and relatively longer daughter axes from the ultimate dichotomy (fig. 6B).

This emendation has resulted in the maximum known length of *S. australis* being reduced from 145 mm to 80 mm and the reduction of known dichotomies to one, with the sporangial dimensions and morphology remaining the same. Specimens attributed to *S. australis* herein (fig. 2A–E) were deposited in a deep marine quiescent environment of the Wilson Creek Shale, and like the holotype, possessed parallel erect axes. This branching architecture of erect parallel aligned axes was found only in three specimens, including the holotype. All the other specimens bar one, which is defined below, are too poorly preserved to attribute to any taxon. Parsimony suggests that parallel axes that dichotomise at the same level, with axes of comparable widths, terminating in elongate sporangia on short daughter axes also of equal dimensions, that have been transported a considerable distance belong to the same plant (*sensu lato* Wang and Hao, 2004; Edwards et al., 2015; Edwards and Li, 2018a) and are representative of its true branching architecture. We acknowledge that we have failed to show organic connection, and current alignment could conceivably result in this axial configuration, but the likelihood of this occurring to three separate specimens with characters such as branching and sporangia occurring at the same height and with the same dimensions is unlikely. We postulate that the parallel aligned axes may have emanated from a rhizomatous region because there was no converging of the parent axes. Two of these parallel aligned specimens were included in Tims and Chambers (1984) but noticeably in both cases, only one of the parent axes was visible (Tims and Chamber, 1984: text-fig. 2A, pl.32, figs. 1, 2, 4). Additionally, the line-drawing of *S. australis* in Tims and Chambers (1984: text-fig. 2a) shows the daughter axes of the parent axes with slightly differing lengths, which was based on Tims and Chambers (1984: pl. 32, fig. 1). But a closer examination of this specimen (holotype; fig. 2D) shows the daughter axes are preserved on different levels of lamina, with the perceived shorter daughter axis (upper arrow) partly obscured by another axis.

The specimens removed from *Salopella australis* (Tims and Chambers, 1984: pl. 32, figs 3, 5) and placed in Gen. et sp. indet. include isolated poorly preserved sporangia from both the Wilson Creek Shale on Frenchmans Spur (fig. 2F, G) and specimens from Limestone Road because the preservations were generally poor and the branching architectures greatly differed to the holotype. One of the excluded specimens (Tims and Chambers, 1984: pl. 32, fig. 3) with differing branching architecture to *S. australis* is described below as a new morphospecies. Thus, *S. australis* is no longer represented in the flora of the Lower Plant Horizon.

Salopella caespitosa Tims and Chambers, 1984 (fig 3A–I (holotype) and fig. 4A–E)

Material: NMV P50016 (holotype) and NMV P235941 both with part and counterpart.

The circumscription of *Salopella caespitosa* was based on a single specimen with its counterpart from the Wilson Creek Shale Formation on Frenchmans Spur Track approximately 10 km west of Matlock in central Victoria. No new data have been added on this taxon since its inception. The discovery of a new specimen from the base of the Humevale Formation on Ghin Ghin Road near Yea preserved in semi-relief contributes information on its dimensions, gross morphology and temporal range.

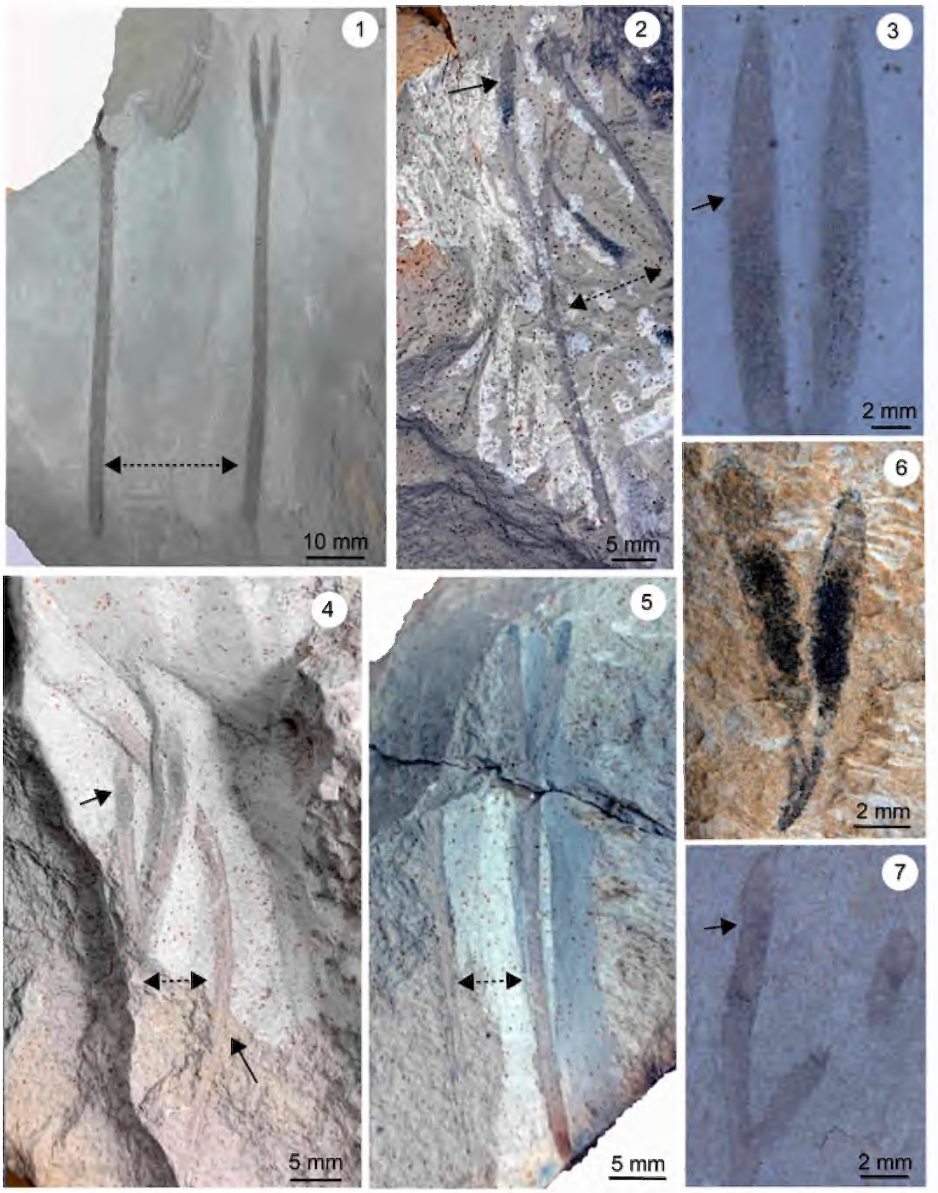

Figure 2. *Salopella australis* displaying parallel parent axes dichotomising into much shorter daughter axes that are terminated with elongate sporangia, delineated with a constriction just above dark sporogeneous region. All from Wilson Creek Shale on Frenchmans Spur track, 10 km west of Matlock. A, erect parent axes parallel to each other, dichotomising into two elongate sporangia from Wilson Creek Shale. Re-photographed here; originally published in Tims and Chambers (1984: pl. 32, fig. 4) and Tims (1980: fig. 4.1.9). Specimen NMV P50014. B, forked dichotomy terminated by sporangia from Wilson Creek Shale. And to the right hand side of the forked axis is another long axis, which based on its orientation may also be part of the same plant. Constriction at arrow, lower arrow at dichotomy and double arrow at two aligned axes. Specimen NMV P33219. C, close-up of fructification in A, sporangia barely extend beyond the confines of their subtending axes, with slight constriction present above sporogeneous region (at arrow). Specimen NMV P50014. D, E, holotype, part and counterpart. On part, constriction at arrow in sporangium. On counterpart, both parent axes are parallel to each other (at dotted arrow). Re-photographed here, originally published in Tims and Chambers (1984: pl. 32, figs. 1, 2). Specimens NMV P50008.1 and NMV P50008.2, respectively. F, Gen. et sp. indet. – short daughter axes terminated in elongate sporangia. The cortex may be absent from subtending axes, with only the central line visible. The lack of cortex prevents assigning to *S. australis* as width of subtending axis to sporangial width is required. Originally photographed by Tims (1980: fig. 4.1.13). Specimen NMV P50010.2. G, *S. australis*, with two short daughter axes, with constriction at arrow of the sporangium, which is the same width as its subtending axis. Specimen NMV P202886.

Description. The new specimen's length is 135 mm and consists of two synchronous dichotomies with longer than wide sporangia terminating each axis. The naked slender axes are 0.8–1.8 mm wide, with the axial width decreasing equally after each dichotomy. The first dichotomy occurs c. 80 mm from the base of the fossil and c. 31 mm from the second dichotomy (fig. 4A at lower arrow). The subtending axes to the sporangia are 0.9–1.0 mm wide and 22–25 mm high with some slight variation in the width along all four axes and a slight narrower evident beneath sporangia three and four (fig. 4B, the subtending axis to sporangium four pinches slightly about 1 mm below the sporangium). The sporangia are fusiform 1.5–2.0 mm wide and 4.8–6.0 mm high with the subtending axis slightly widening into the base of each sporangium. The widest part of the sporangia occurs in the lowest quarter length, followed by a gentle tapering to rounded sporangial tips. A sporangial wall is evident primarily but is not confined to the basal parts of the sporangia measuring 0.2–0.3 mm wide and is continuous with the subtending axes. Sporangia two, three on the part and four on the counterpart possess what appears to be an infilled oval presumed sporogenous area, which are no greater than 1.2 mm wide and 1.5 mm high. Sporangium four on the counterpart shows a fine linear cavity 0.15 mm wide entering the base of the sporogenous area and sporangium three on the part shows similar but larger opening beneath the sporogenous area, and beneath this is a fine central axis 0.1 mm wide; beneath sporangium two on the subtending axis, this axis is 0.2 mm wide. Sporangium two (part) upper half possesses longitudinally oblique striations, 0.06–0.6 mm apart.

Remarks. Comparison to holotype. The new specimen measures 50 mm longer than the holotype (fig. 3), and its axial width is broadly in range with the holotype, which measures 1.1–1.9 mm wide according to Tims and Chambers (1984). What appears to be the widening of the parent axis in the specimen (fig. 4A) is where the first dichotomy occurs, with the two daughter axes aligned for 26 mm before diverging for the remaining 5 mm before the second dichotomy. From the holotype, the best examples of branching to compare to the specimen were found on the part specimen (right-hand side) with isotomous dichotomies subtending sporangia one–seven (fig. 3A, fig. 6D). Proximally on the axes ultimately terminate in sporangia one–seven show the axes emanating from a horizontal axis. This horizontal axis may represent part of a rhizomatous system or a distorted axis. Tims and Chambers (1984) appear to have considered this a dichotomy because no other part of the fossil would give three dichotomies. However, it is equivocal as to whether it is a distorted axis with a dichotomy. Nonetheless, the axes of the new specimen examined are noticeably less flexuous than the holotype; for example, on the holotype axes leading to sporangia eight and nine showing changes in orientation of about 45° in conjunction with the daughter axes of dichotomies occurring at 10° and 45°. These differences possibly represent differences in both current strength during deposition and the level of degradation of each of the plants. There is a noticeable variation in the distance between the ultimate branching points and sporangia in the holotype, from c. 6 mm as seen in sporangium 12, to c. 26 mm for sporangium seven, and up to at least 57 mm for sporangium eight, where the presumed branching point is not visible. The axes decreased after each dichotomy, as noted by Tims and Chambers (1984), but with the specimen examined herein there is a much greater decrease in axial width after the first dichotomy. Examination of the holotype did reveal a slight narrowing in the subtending axes (fig. 3D–F) of most of the sporangia (Tims and Chambers 1984: pl. 34, fig. 3); this was observed beneath two of the sporangia on the specimen, but in both cases may be artefacts of preservation, and more specimens are required to confirm this character.

The size range of the sporangia in the holotype, 3.2–6.0 mm high and 1.3–2.0 mm wide (Tims and Chambers, 1984), is similar to the specimen examined herein, and both have a comparable average height to width ratio of 2.6 (Morris and Edwards, 2014: table 3) for the holotype and 3.2 herein. The holotype shows slight variation in the location of the widest point of the sporangia, occurring either in the lowest quarter (fig. 4F), like with NMV P235941 (fig. 4C) or midway (fig. 3D). The minor difference is possibly accounted for by the different types of preservation. The specimen NMV P23591 shows these sporangial bodies in semi-relief and indicate they were not flattened bodies. Furthermore, examination of sporangia of the specimen revealed an oval presumed sporogenous region in the basal part of the sporangia, which is also present on sporangium 13 of the holotype (fig. 3H). Tims and Chambers (1984: pl. 33, figs 3–4) noted that on sporangium 13 of the holotype it may either be a double sporangium or dissociation of the sporangial wall giving the appearance of a double sporangium. The evidence of a sporogenous area basally and relatively thick sporangial walls from the specimen examined herein (fig. 4B) suggests either a crushed sporangium or stage of senescence pertaining to dehiscence. Furthermore, some of the sporangia in the holotype have a darkened presumed sporogenous area completely filling insides of the sporangia (fig. D–F), which may have resulted from the breakdown of the wall holding the sporogenous area prior to fossilisation, as the sporogenous area occurs as a basal oval body on all sporangia of the specimen examined.

Tims and Chambers (1984: pl. 33, fig. 3) found central lines of 0.2 mm diameter throughout the specimen, one of which was beneath sporangium 13. On the specimen NMV P235941, the central line was found to connect to base of the sporogenous region (fig. 4B, C), which Tims and Chambers (1984) had postulated. Tims and Chambers (1984) noted some axes of the holotype to dichotomise (c. 6.0 mm) relatively close to the base of the sporangia (fig. 3C); however, this was not the case with NMV P235941.

The presence of longitudinal oblique striations on the upper half of sporangium two may reflect cell orientation and possible twisting as a means of dehiscence. Obliquely orientated cells in the sporangia have been recorded for some *S. allenii* and absent for *S. marcensis* (Fanning et al., 1992; Morris and Edwards, 2014), and throughout the entire sporangia and subtending axes of *Tortilicaulis* (Edwards et al., 1994). There was no indication of twisting found for the subtending axes of the specimens' sporangia, suggesting it may only affect the upper part of the

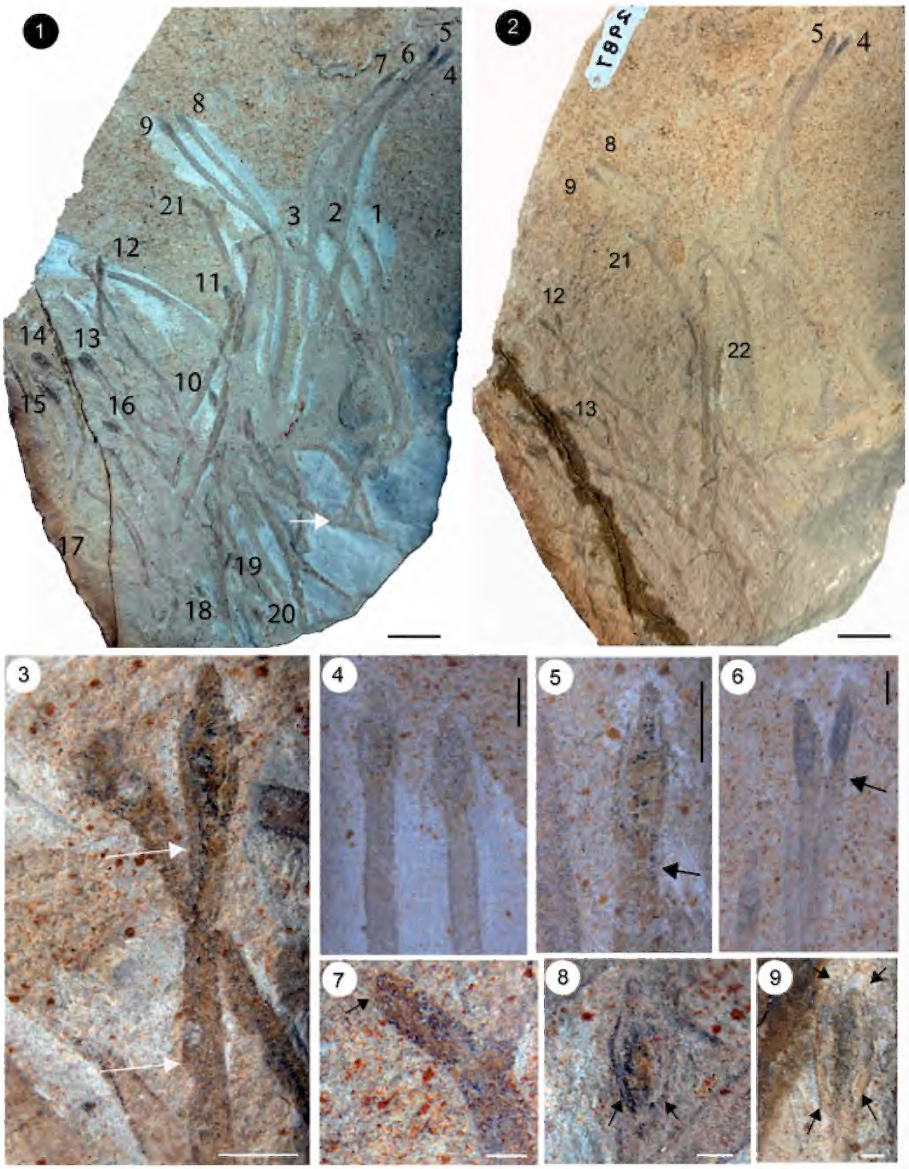

Figure 3. *Salopella caespitosa* (holotype) from Wilson Creek Shale on Frenchmans Spur track, 10 km west of Matlock. A, B, part (NMV P202987.1) and counterpart (NMV P202987.2), respectively; numbering follows Tims and Chambers (1984, pl. 33, fig. 1). Counterpart images are reversed to be in the same orientation as the part specimen. A, on right-hand side of part specimen, double isotomous dichotomies lead to sporangia one–seven. Note, at the arrows, there is perpendicular branching that is suggestive of a rhizomatous system. C, sporangium 12; at the arrow there is another axis that is terminated in a sporangium that is partially visible. Specimen NMV P202987.1. D–F, Evidence of a slight constriction beneath sporangia at arrows. D, sporangia eight and nine (on the left). Widest part of each sporangium occurring approximately midway along their length. Note, rephotographed; originally published in Tims and Chambers (1984: pl. 34, fig. 3). Specimen NMV P202987.1. E, sporangium 22 is c. 4.06 mm long and 1.4 mm wide. The axis decreases from 1.2 mm proximally to 0.5 mm just beneath the sporangium. Specimen = NMV P202987.2. F, sporangia four (right) and five, both sporangia are slightly wider in the lower quarter of each sporangia. Specimen = NMV P202987.2. G, sporangium 22, appears to be two immature sporangia juxtaposed. At arrow, the apex (rounded) of the smaller fusiform sporangium is apparent. Specimen NMV P202987.1. H, sporangium two, lower arrow at walls surrounding presumed oval sporogeneous area, which reaches approximately halfway the length of the sporangium to the upper arrow. Specimen NMV P202987.1. I, sporangium 13, arrows at walls surrounding sporangeneous area and upper arrow showing extent of oval sporogenous body. The walls does not recombine apically like in sporangium two, suggesting it may have been crushed, or hidden, beneath the matrix. Rephotographed; originally figured by Tims and Chambers (1984: pl. 33, fig. 3). Specimen NMV P202987.2.

sporangia; however, this is conjectural. As noted by Morris and Edwards (2014: 42), sporangia containing spores are required for unequivocal identification and assessment of relationships. While the specimen described is three-dimensionally preserved, we believe erecting a new taxon to segregate it from the form genus would be premature and we should wait for more data. The presence of this specimen at the base of the Humevale Formation potentially suggests a late Silurian age (Rickards, 2000). However, as outlined in the stratigraphy section, we suggest a Lower Devonian age range for specimens found at Ghin Ghin Road until unequivocal evidence of age becomes available.

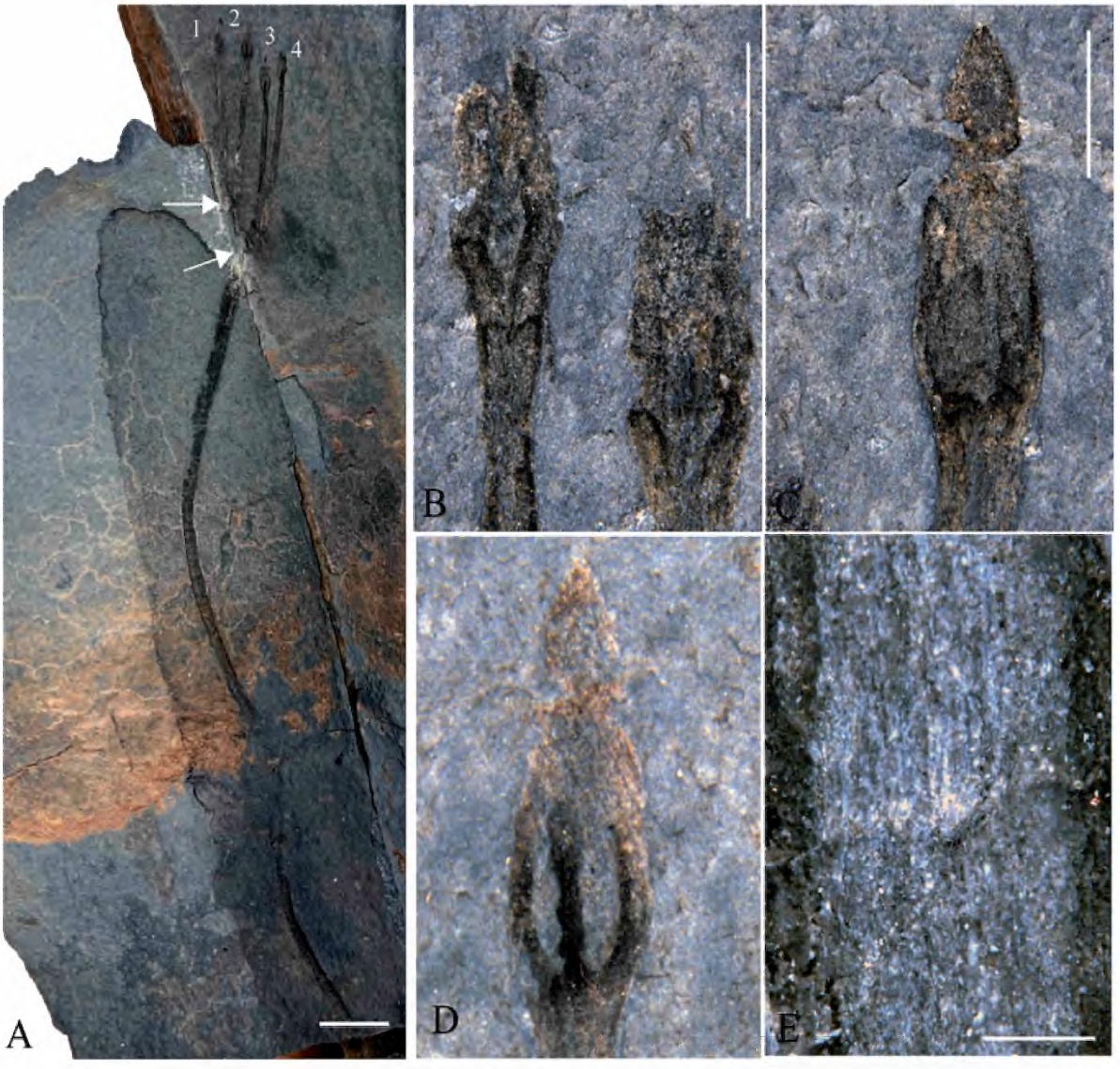

Figure 4. *Salopella caespitosa* NMV P235941 from Devil's Elbow on Ghin Ghin Road, northwest of Yea. A, overview of whole specimen. NMV P235941.1. B, arrow (Vt) at vascular trace entering base of oval presumed sporogenous body of sporangium four, and the subtending axis to sporangium four pinches slightly about 1 mm below the sporangium. Lower arrow at region where subtending axis is continuous with sporangial wall and upper arrow shows extent of sporangial body of sporangium three. Note, for both sporangia, the distal parts appear to be hidden in the matrix. NMV P235941.2. C, lower arrow (Vt) at vascular trace entering base of oval sporogenous body, with upper arrow at distal extent of sporogenous body on sporangium two on the counterpart. Note, no longitudinally oblique striations are evident in upper half of sporangium but are evident on the part specimen. NMV P235941.2. D, sporangium two at arrow longitudinal oblique striations on the upper half of the sporangium. NMV P235941.1. E, close-up of parent axis with longitudinal striations. NMV P235941.1.

Plantae. *Incertae sedis*

Genus. *Salopella* **Edwards and Richardson, 1974**

Salopella laidae McSweeney, Shimeta and Buckeridge, sp. nov. (fig. 5A, B, fig. 6D)

Salopella australis Tims and Chambers (1984: pl. 32, fig. 3, text-fig. 2C)

Diagnosis. Plant at least 55 mm long, tuft branching architecture, with sporangia all reaching the same height, with naked dichotomously synchronous branched axes up to 3.2 mm wide basally and 1.3 mm below sporangia. Axial width decreases after each dichotomy. Isotomous branching angles small, 30°–40° for the ultimate dichotomies and 15°–50° for basal dichotomies. At least two orders of branching. Branching 10.0–14.0 mm below sporangia. Eight sporangia, elongate subfusiform 9.7–11.0 mm high and up to 2.5 mm at widest section in mid region, and wider than subtending axes, obtuse apices.

Etymology. Named for Mrs Peg Laid who kindly gave permission to collect fossil specimens from her property on Ghin Ghin Road, Yea.

Holotype. NMV P50011.1 and NMV P50011.2, part and counterpart respectively, figured by Tims and Chambers, 1984: pl. 32, fig. 3 and text-fig. 2C

Locality. Location 4, Brackley's cutting (Harris and Thomas, 1941) Limestone Road, 2 km southeast of Yea. Note: exposure referred to as locality 62 in Couper (1965). 37° 12.38' S, 145° 25.39' E.

Stratigraphy and age. Location 4 (Harris and Thomas, 1941: 303) Yea Formation (Garratt 1978), Lower Devonian (Pragian; Edwards et al., 1997; Rickards, 2000; Rickards and Garratt, 1990).

Salopella laidae sp. nov. **(fig. 5A, B, fig. 6C)**

Description. Specimen preserved as a faint white compression on blue-grey claystone with six of the eight sporangia preserved. There is no clear sporogenous area within the sporangia. However, sporangia five, seven and eight (fig. 6C) on the part (fig. 5A) possess darkened creamy-grey regions extending up two-thirds of their lengths and possibly represent a sporogeneous region. No internal anatomy or spores were

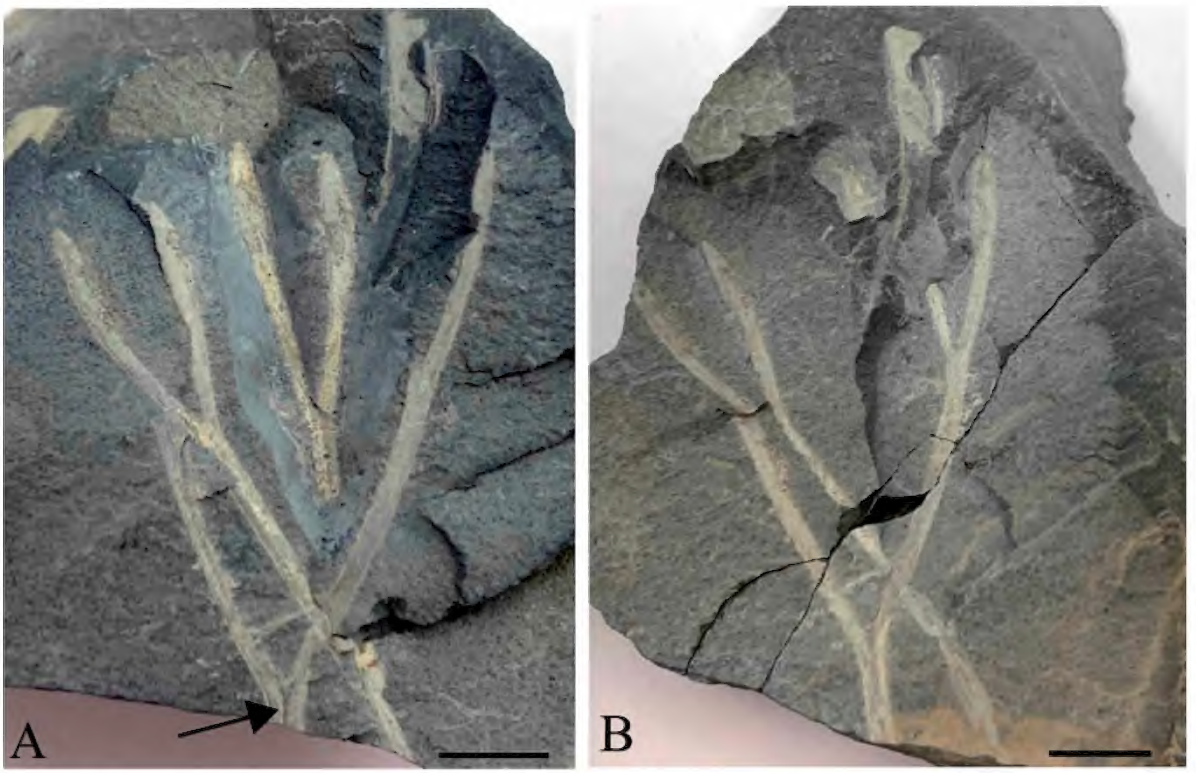

Figure 5. *Salopella laidae* sp. nov. (holotype) NMV P50011.1 and NMV P50011.2, part and counterpart, respectively, with counterpart reversed to be in the same orientation as part specimen. From location 4 (Brackley's cutting) on Limestone Road, Yea. A, double isotomous dichotomy visible, terminated with eight elongate sporangia, five visible. At lower arrow central line and at F, folding of tissue. On sporangium seven ?sporogenous region highlighted. Rephotographed; originally figured by Tims and Chambers, 1984: pl. 32, fig. 3 and text-fig. 2C. B, arrow at daughter axis missing on part present.

recovered when Tims and Chambers (1984) examined this specimen. The sporangia are slightly wider than the widths of their subtending axes and do not taper distally but come to a rounded apical region. There are two synchronous dichotomies clearly visible, with the axial width decreasing only after each dichotomy. Folding of tissue appearing as a longitudinal lineation along the edges of the axes and sporangia are visible; no evidence of dehiscence mechanism is present (fig. 5A).

Comments and comparison with other species. The diagnosis and description of this taxon is based on one specimen (part and counterpart). While we are mindful of issues in naming a new species on one specimen, we have done so because of the shape of the sporangia and compact branching architecture that set it apart from other rhyniophytoids (Table 1). The use of the paraphyletic genus *Salopella* (Edwards et al., 1994) is to emphasise its gross morphology and to follow previous workers (Tims and Chambers, 1984) in identifying Victorian flora. However, we note that work done by Edwards et al. (1994) on in situ *Salopella* spores demonstrated significant diversity, that can be difficult to ascertain because of convergence of some sporangial shapes (Edwards et al. 2001: 11), making assertions on palaeogeographic distribution and spread unwise without palynological evidence. Tims and Chambers (1984) originally assigned this specimen to *S. australis*, but *Salopella laidae* sp. nov. differs to *S. australis* in a number of its characters (fig. 6 – comparative line drawings of Australian *Salopella*). *Salopella laidae* sp. nov. possesses sporangia that are clearly delineated from their subtending axes, differing noticeably from coeval *S. australis* (fig. 2A–E) where the sporangia are as wide as their subtending axes. Furthermore, the sporangia in *S. laidae* sp. nov. do not taper from half-way to one-third from their apices as in *S. australis*; instead, they hold their sporangial widths before terminating with rounded apices. While the sporangial apices appear obtuse, this cannot be assumed to have been the case in life, as Morris and Edwards (2014: 40) found when examining *S. allenii* that compressed specimens possessed rounded apices of varying degrees, except that one specimen of *S. allenii* that was preserved in 3D had a pointed apex. The parent axes leading to the ultimate dichotomy in *S. australis* are long, erect and aligned parallel to each other (fig. 2A), being easily distinguished from *S. laidae*, where the axes leading to the ultimate dichotomy are at an angle to the vertical. Furthermore, *S. australis* only possesses one dichotomy, while *S. laidae* possesses two, or possibly three, as suggested in Tims and Chambers (1984: text-fig. 2C). However, it should be noted the proximal axes of *S. laidae* sp. nov. are orientated away from each other, suggesting they may have come from a rhizomatous axis instead of a dichotomising one.

One of the parent axes of *S. laidae* sp. nov. is incomplete, but likely possessed four sporangia (fig. 6C). This is based on the relative dimensions, orientation and positions of both parent axes to each other, and that four sporangia terminate the daughter axes of the other parent axis.

The sporangia of *Salopella caespitosa* are ovate to fusiform and up to 6.0 mm high and 2.0 mm wide (Tims and Chambers, 1984), which is approximately half as high than *S. laidae*. Furthermore, the axes of *S. caespitosa* are more gracile than those of *S. laidae*, as the latter reached a maximum width of 1.9

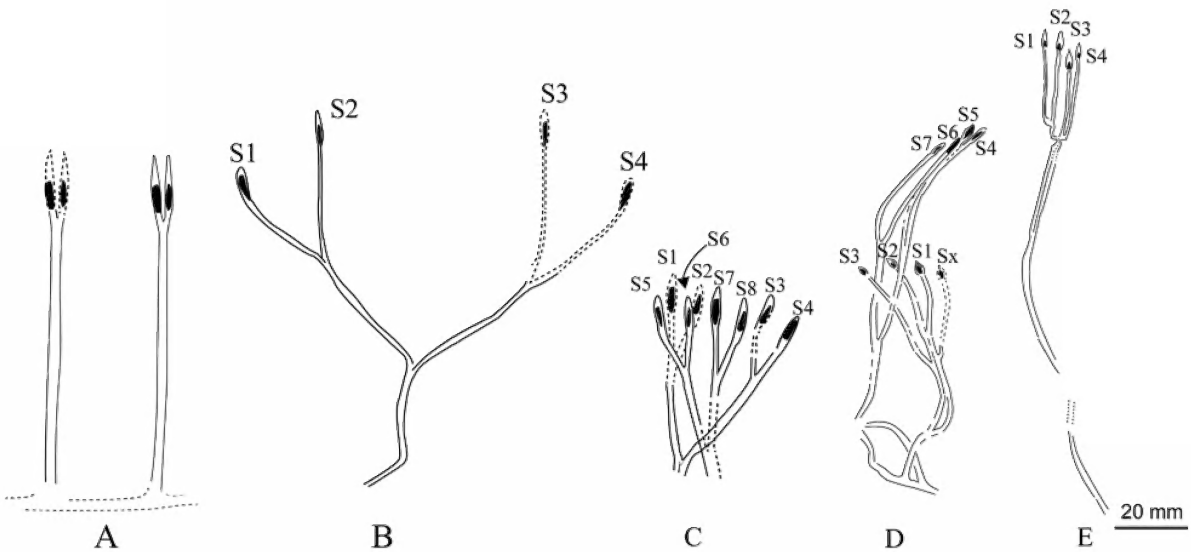

Figure 6. Line-drawings of Victorian early land plants with longer than wider sporangia. **A,** *Salopella australis* from Wilson Creek Shale on Frenchmans Spur track, near Matlock. Specimen NMV P50014. **B,** Gen. et sp. indet. from Limestone Road, Yea. Originally placed in *S. australis* but branching architecture clearly differs. Specimen NMV P157323. **C,** *Salopella laidae* sp. nov. from Limestone Road, Yea. NMV P50011. **D,** *Salopella caespitosa* (holotype) from Wilson Creek Shale on Frenchmans Spur track, near Matlock. Specimen NMV P202987. **E,** *Salopella caespitosa* from Ghin Ghin Road, Yea. Specimen NMV P235941.

mm proximally and 1 mm beneath the sporangia, whereas for *S. laidae* axes were at least 3.2 mm proximally and 1.3 mm beneath the sporangia. In comparison to other *Salopella* globally, the sporangia of *S. marcensis* and *S. xinjiangensis* are much smaller than *S. laidae*, reaching a maximum length of 3.4 mm and 3.5 mm long, respectively, and both much narrower (Morris and Edwards, 2014: table 3). Moreover, the sporangia of *S. xinjiangensis* are tongue-shaped (Cai et al., 1993; Dou and Sun, 1983), but *S. marcensis* sporangia are similar in gross morphology to *S. laidae*, being elongate and tapered at their apices according to Fanning et al. (1992). *Salopella marcensis* are much smaller plant than *S. laidae*, reaching 6.38 mm high, while *S. laidae* reached at least 55 mm high (Fanning et al., 1992: 174). While disarticulation for *S. marcensis* during transport seems likely, the isotomously branched axes bearing the sporangia for *S. marcensis* are much smaller than for *S. laidae*, ranging 0.05–0.5 mm wide (Fanning et al., 1992).

In Fanning et al. (1992: fig. 35), there is a silhouette of *S. marcensis* that shows a sporangium occurring on a lateral axis below a further bifurcation, indicating in this case at least that sporangia did not necessarily occur at approximately the same level, as is the case with *S. laidae* sp. nov. Finally, the type species of *Salopella*, *S. allenii* possessed fusiform or spear-shaped sporangia (Edwards and Richardson, 1974; Morris and Edwards, 2014) – significantly different to those of *S. laidae* sp. nov.

Discussion

Edwards and Richardson (1974) established *Salopella* based on one Lochkovian specimen of *Salopella allenii* from Brown Clee Hill, Shropshire (England); they noted its affinities to Rhyniaceae and that *S. allenii* possessed axes with dimensions that were between the range seen for *Rhynia gwynne-vaughani* and *R. major* (= *Aglaophyton majus*), with sporangia similar to both but lacking internal anatomy as seen in the Rhynie chert specimens (Edwards et al., 2017). Various workers have hypothesised that rhyniophytes/rhyniophytoids occupied ephemeral ruderal terranes, such as wetlands and deltas, whereby the rhyniophytes/rhyniophytoids completed their life cycles over short periods (Edwards, 2003; Edwards and Davies, 1990; Morris et al., 2011; Raymond et al., 2006; Wellman et al., 2000), possibly with some forming dense monotypic stands, such as the well-preserved aligned axes found near a fossilised channel from the Lower Old Red Sandstone deposits of Brecon Beacons (Edwards and Fanning, 1985: 156). According to Lavender and Wellman (2002), Edwards and Richardson (2004), and Raymond et al. (2006), seasonal conditions would have suited the short life cycles of rhyniophytes/rhyniophytoids. The location of the Melbourne Zone c. 30° south of the equator during the Lower Devonian (Torsvik and Cocks, 2019: fig. 9) suggests that the terrestrial sources for these deposits were likely also influenced by a seasonal climate, suiting the short life cycle of rhyniophyte/rhyniophytoids.

Furthermore, Edwards and Richardson (2004), when investigating the Lower Devonian calcrete palaeosols on the Avalonian Terrane, proposed rhyniophytes/rhyniophytoids as likely pioneer taxa because they were found on calcrete palaeosols that had formed in unstable interfluvial areas, with more advanced coeval plants, such as the zosterophylls or lycopsids, inhabiting more stable terranes to better accommodate their longer life cycles (Wellman et al., 2000). According to Powell et al. (2003: 29), there was a gradual shallowing of marine facies from the western margins of the Melbourne Zone in the Darraweit Guim Province, and eastward movement of the shoreline during the upper Silurian–Lower Devonian, which may have provided similar unstable conditions for rhyniophytes/rhyniophytoids, because palaeocurrents at areas in Yea and Matlock indicate a west or southwesterly source from the western parts of Victoria, which was terrestrial at the time (Powell et al., 2003: 23). Edwards and Davies (1990: fig. 16.3) noted the decline of rhyniophytes/rhyniophytoids from Laurussian sites during the late Pragian and Emsian stages of the Lower Devonian, possibly due to the proliferation of zosterophylls early in the Devonian. It is possible the uplift of the Tabberaberan highlands towards the end of the Lower Devonian in Victoria (Powell et al., 2003: 32) may have provided ideal unstable conditions for rhyniophytes/rhyniophytoids into the Emsian but work on the palaeoflora from the Norton Gully Sandstone Formation has been limited.

Finally, there is a noticeable difference in the number of rhyniophyte/rhyniophytoid taxa from Yunnan, China, in what was once part of the South China Block located at and north of the equator during the Lower Devonian (Torsvik and Cocks, 2019: fig. 9a), and those found in the *Baragwanathia* floral assemblage. According to Hao and Xue (2013: fig. 5.3), rhyniophytes/rhyniophytoids make up a small percentage (c. 2.7%) of the taxonomic groups found in the Posongchong Flora. Recently, Edwards and Li (2018b) erected *Polycladophyton gracilis* and *Jiangyounia gengi* possessing a grade of organisation belonging to Rhyniophytina. However, *Salopella* specimens have not yet been recovered (Hao and Xue, 2013: 193), suggestive of some level of isolation between the two regions.

Conclusions

Defining taxa based on gross morphological characters alone has limitations because it excludes cryptic characteristics and likely results in one morphospecies encompassing a number of distinct species. However, this study and the work of Tims and Chambers (1984) has provided a morphological framework from which new Victorian taxa may be defined, providing an impetus for further research.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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